Preface

In 2020, volume 103 of the Journal had 12 papers, 1 book review, 1 comment and John Glover's obituary—the most articles since volume 98 (2015) in which there were 18 papers and 2 book reviews.

During the year the Society held two symposia: 'Wallacea: connecting Asia to the Australian continent' on 14–15 February and 'Western Australia's marine and estuarine environment' on 3 October. Volume 103 includes the first two articles from the former symposium, a comment on one of these and a review of various books on Wallace—all of which follow a history-of-science theme. Also in this volume are the last two articles from the 2018 symposium on 'Landscapes, seascapes & biota: unique WA – past, present & future', which yielded eight papers for the journal. Of those, the paper by Don McFarlane *et al.* in volume 103—'Runoff and groundwater responses to climate change in South West Australia'—presents an overview of one of the most serious challenges for the State: the drying climate in the Southwest. Other articles in this volume cover diverse topics: the Bassendean soil, seagrass and macroalgal biogeography, tiger snakes on Carnac Island, Noongar lizard traps near Albany, modern foraminifera in Southwest estuaries, birds on Faure Island in Shark Bay, the greater bilby in the Pilbara, biota of Gibson Desert rock pools and *Daviesia* cluster roots.

Further symposia are planned: early in 2021 on 'Swan Coastal Plain – temporal and special patterns', and later in the year the inaugural John Glover Symposium to honour his generosity to the Society.

With the transition to open access and online publishing the journal no longer has parts so all articles are published in the order they become finalised. Supplementary data are either included as appendices or as an associated file; the former is preferred unless such data are overly large.

Proposal for a new Bassendean reference soil in Western Australia

BENJAMIN L TURNER [1,2*] & ETIENNE LALIBERTÉ [2,3]

[1] *Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama*

[2] *School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley, Perth, WA 6009, Australia*

[3] *Institut de recherche en biologie végétale, Département de sciences biologiques, Université de Montréal, 4101 Sherbrooke Est, Montréal H1X 2B2, Canada*

**Corresponding author:* ✉ *TurnerBL@si.edu*

Abstract

Soils on the Lower Pleistocene Bassendean sands of the Swan Coastal Plain of Western Australia are among the most infertile in the world, but support plant communities of remarkable diversity. Following detailed studies of soil chronosequences in the Perth region, the current Bassendean reference soil near Yalgorup National Park appears to be on a Middle Pleistocene Spearwood dune, rather than a Lower Pleistocene Bassendean dune. This assessment is based on the bright yellow subsoil, rather than the bleached quartz sand that characterises soils on Bassendean sand. We therefore propose a new location for the Bassendean reference soil, on Lower Pleistocene dunes in the Yeal Nature Reserve north of Perth. The site forms part of the Guilderton soil chronosequence and the extensive Bassendean dunes in this region retain a distinct dune morphology. The proposed reference soil consists of many metres of medium and coarse-grained bleached quartz sand with extremely low total P concentrations (<3 g P m^{-2} in the upper metre). The profile provides an exemplary Bassendean soil suitable for the regional reference, and demonstrates the consequences of long-term pedogenesis on the Swan Coastal Plain.

Keywords: Bassendean, chronosequence, Entisol, Guilderton, Podzol, reference soil, Sand, Swan Coastal Plain

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INTRODUCTION

Southwestern Australia is known for its ancient landscapes, diverse plant communities, and infertile soils. Some of the most infertile soils are on the Swan Coastal Plain, associated with three major sand deposits formed by Quaternary interglacial sea-level high stands (McArthur 2004; Laliberté *et al*. 2012; Turner & Laliberté 2015; Turner *et al*. 2018). Soils on these deposits form a chronosequence, with Holocene soils on Quindalup dunes (Safety Bay Sand), Middle Pleistocene soils on Spearwood dunes (Tamala Limestone) and Lower Pleistocene soils on Bassendean dunes (Bassendean Sand, on the Ascot Formation; Laliberté *et al*. 2012; Turner *et al*. 2018). Long-term pedogenesis involves acidification and leaching of carbonate from Holocene soils, followed by leaching of iron oxides from Middle Pleistocene soils, leaving Lower Pleistocene soils consisting of bleached quartz sand profiles many metres deep (Turner & Laliberté 2015; Turner *et al*. 2018). These Bassendean soils are among the most infertile soils in the region, if not the world. They are of particular significance ecologically because they support some of the highest-diversity plant communities in Western Australia (Laliberté *et al*. 2014; Zemunik *et al*. 2015, 2016).

The soils of southwestern Australia were described in detail by McArthur and colleagues (McArthur & Bettenay 1974; McArthur & Russell 1978), including the identification of a series of reference soils (McArthur 2004). Their work provided the foundation for understanding soil development on the Swan Coastal Plain and guided us during our recent studies of soil chronosequences in the region (Laliberté *et al*. 2012; Hayes *et al*. 2014; Turner & Laliberté 2015; Zemunik *et al*. 2016; Turner *et al*. 2018). These studies include soils of the coastal sandplains from Jurien Bay in the north to D'Entecasteaux National Park in the south (on the Scott Coastal Plain). Our primary aim was to identify soil chronosequences that would allow us to examine relationships between soil development and biological communities during long-term ecosystem development (e.g. Laliberté *et al*. 2017; Turner *et al*. 2019).

During our research, we revisited several of McArthur's reference soil locations near Yalgorup National Park. However, we interpret the Bassendean reference soil (SCP 11 in McArthur 2004) as having been formed on a Middle Pleistocene Spearwood dune. The SCP 11 site was located in the Buller Nature Reserve, just south of Buller Road near the town of Waroona (32.86740°S, 115.82908°E). McArthur reported that the profile consisted of a 50 cm-thick, bleached grey A horizon over light yellowish brown (10YR 6/4) to yellowish brown (10YR 5/6 and 5/8) sand, with no spodic horizon in the upper 180 cm. However, the yellow is due to iron oxide coatings on sand grains and is characteristic of soils of the Spearwood dunes. The profile is similar to a Middle Pleistocene profile nearby on a Spearwood

dune, termed the old Spearwood profile in Turner *et al*. (2018). In contrast, the much older Bassendean soils have lost iron oxides from the entire profile, yielding bleached grey/white sand many metres deep.

We are confident that we examined the same soil described by McArthur (McArthur 2004) and our observations by auger match the original description of the SCP 11 reference soil. The site is close to an extensive area of Bassendean soils to the east on flat terrain, although this is now almost all converted to agricultural land and little natural vegetation remains, perhaps explaining why McArthur positioned the reference soil at this location. We identified an area of Bassendean soil under native vegetation nearby in the Buller Nature Reserve (about 1.7 km to the SSE, 32.88197°S, 115.83583°E), which we included in the Yalgorup chronosequence (Turner *et al*. 2018). However, this site was probably influenced to some extent by nearby farmland, reflected in a slightly greater total P concentration than typical of Bassendean profiles elsewhere.

Given that the location of the current Bassendean reference soil appears to be on a Spearwood dune, we propose an alternative site for the Bassendean reference soil (Fig. 1). There is an appropriate profile in the Yeal Nature Reserve south-west of Guilderton, approximately 70 km north of Perth, which contains an extensive area of Bassendean soil (Fig. 2). This profile was previously included in a publication describing a series of 2 million-year chronosequences, where it was assigned to stage six of the chronosequence (Turner *et al*. 2018). Here we describe the profile in detail and provide comprehensive information on its physical and chemical properties. The profile represents an exemplary Bassendean soil that is suitable as a new reference for the region.

METHODS

Location and sampling

The proposed Bassendean reference soil is adjacent to the Gnangara–Moore River State Forest on the Swan Coastal Plain north of Perth, Western Australia at 31.39909°S, 115.76005°E (Fig. 1), and is 71 m above sea level. On 16 August 2013, during winter, we excavated a profile pit to approximately 2 m on the upper backslope of the dune. The profile (Fig. 2a) was described by genetic horizon and samples taken for physical and chemical analysis. Deeper samples were obtained using a sand auger by

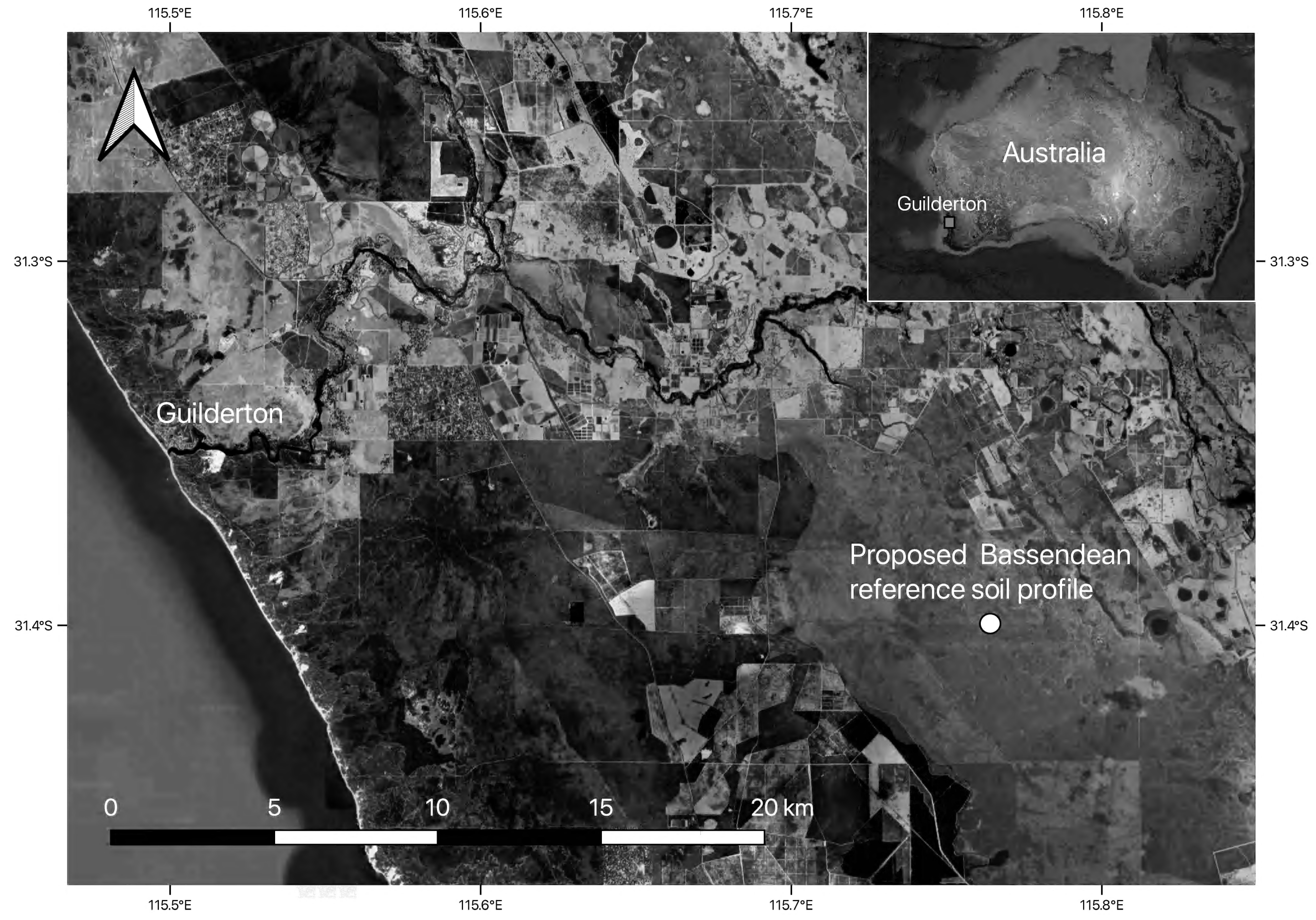

Figure 1. Location of the described profile for the proposed Bassendean reference soil for Western Australia (white circle). The boundary of the Bassendean Soil System is in red (Soil Landscape Mapping – Systems DPIRD-064 dataset, Western Australian Department of Primary Industries and Regional Development; https://catalogue.data.wa.gov.au/dataset/soil-landscape-mapping-systems). Arrow points toward the north. Projected spatial reference system: EPSG:3857. Basemap: Google Inc.

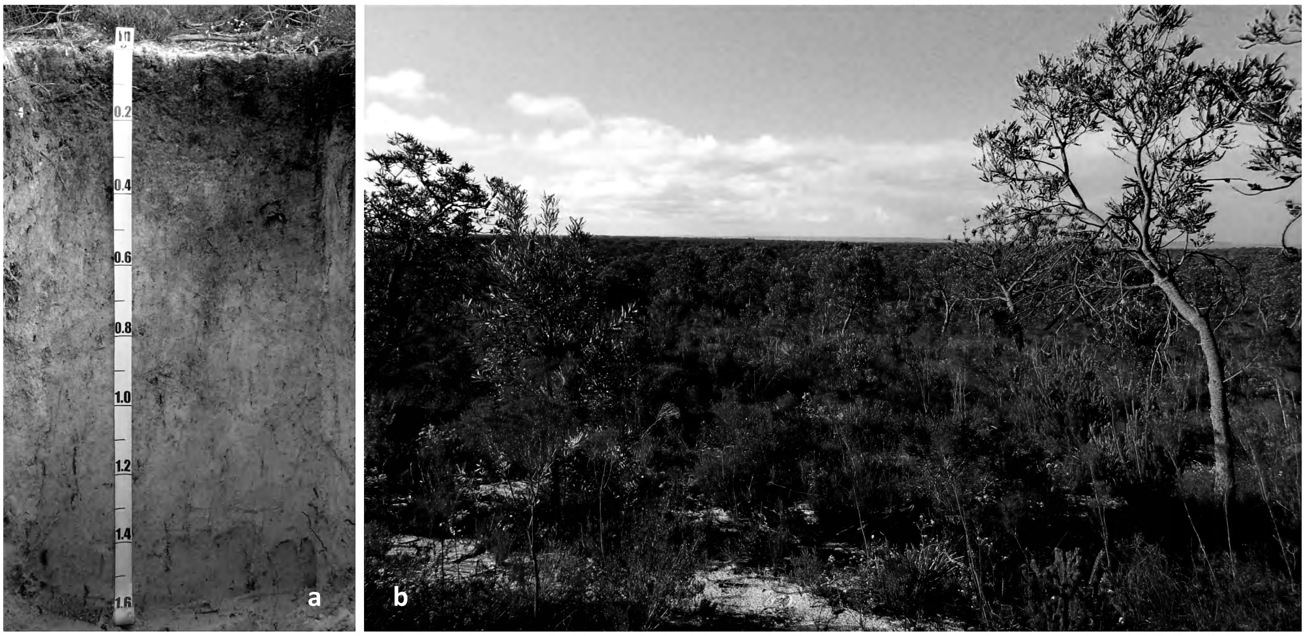

Figure 2. a) The proposed Bassendean reference soil for Western Australia, and b) its landscape position and vegetation.

augering through the base of the profile pit. However, we could not retrieve samples deeper than 5 m due to the incoherent nature of the sand, despite adding water to the auger hole. The soil was classified according to Soil Taxonomy (Soil Survey Staff 1999) and the Australian Soil Classification (Isbell 2002). We do not have soil temperature data for the chronosequences, but estimate the soil temperature regime from air temperatures at Guilderton Aerodrome (data from 1996–2015). The control section for the profile (Soil Taxonomy) is between 30 and 90 cm below the soil surface.

Laboratory Analysis

Following the analytical methodology previously described by Turner & Laliberté (2015) and Turner *et al.* (2018), soil pH was determined in both deionised water and 10 mM $CaCl_2$ in a 1:2 soil to solution ratio using a glass electrode. The concentrations of sand (53 μm to 2 mm), silt (2–53 μm), and clay (<2 μm) sized particles were determined by the pipette method following pretreatment to remove soluble salts and organic matter (Gee & Or 2002), with further separation of sand fractions by manual dry sieving. Total carbon (C) and nitrogen (N) were determined by automated combustion and gas chromatography with thermal conductivity detection using a Thermo Flash 1112 elemental analyser (CE Elantech, Lakewood, NJ, USA). Total phosphorus (P) was determined by ignition (550°C, 1 hr) and extraction in 1 M H_2SO_4 (16 hr, 1:50 soil to solution ratio). Exchangeable cations were determined by extraction in 0.1 M $BaCl_2$ (2 hr, 1:30 soil to solution ratio), with detection by inductively-coupled plasma optical-emission spectrometry (ICP–OES) on an Optima 7300 DV (Perkin-Elmer Ltd, Shelton, CT, USA; Hendershot *et al.* 2008). Total exchangeable bases (TEB) was calculated as the sum of charge equivalents of calcium (Ca), potassium (K), magnesium (Mg), and sodium (Na); effective cation exchange capacity (ECEC) was calculated as the sum of the charge equivalents of aluminium (Al), Ca, iron (Fe), K, Mg, manganese (Mn), and Na; base saturation was calculated by (TEB ÷ ECEC) × 100. Bulk density was determined by taking three replicate cores of known volume in each horizon using a 7.5 cm diameter stainless steel ring and determining the soil mass after drying at 105°C. Total mineral elements were determined by digestion in concentrated (70%) HNO_3 under pressure at 180°C in PTFE vessels (PDS-6 Pressure Digestion System, Loftfields Analytical Solutions, Neu Eichenberg, Germany), with detection by ICP–OES. This also provided a second measurement of total P.

RESULTS

Soil forming factors

The five soil-forming factors are climate, parent material, topography, organisms, and time (Jenny 1941). Mean annual temperature at the site is 18.4°C. The monthly mean minimum temperature is 12.3°C in July and the monthly mean maximum temperature is 25.2°C in January. Mean annual precipitation (mm) 653.4 mm, of which 15% falls in the dry season from November to April inclusive (defined as months with <30 mm rainfall). Potential annual evapotranspiration is 1403 mm, with an annual water balance of –750 mm (Turner *et al.* 2018). The soil moisture regime is therefore xeric and the soil temperature regime is thermic. The parent material is Bassendean Sand, which we assume is approximately 2 million years old based on the age of the underlying Ascot Formation (Kendrick *et al.* 1991). The profile was located on the shoulder of a broad, low dune ridge, facing northeast (5% slope; Fig. 2b). The vegetation is

undisturbed Mediterranean shrubland known locally as kwongan (Lamont *et al*. 1984; Lambers 2014), with scattered *Banksia attenuata* and *B. menziesii* up to 3 m tall, a sparse shrubby understory (~50% cover), and a thin layer of dry leaf litter with approximately 25% bare ground. Roots were present throughout the profile to at least 300 cm.

Profile description

A1—0 to 1 cm; light grey (10YR 7/1) sand; loose, single grain; medium and coarse clean quartz sand grains; abrupt smooth boundary.

A2—1 to 18 cm; very dark brown (10YR 2/2) loamy sand; weak very coarse blocky structure held by very fine sand-binding roots, breaking under moderate force to single grain; moist; medium and coarse clean quartz grains; common coarse, medium, and fine, and many very fine roots; many cluster roots; clear smooth boundary.

A3—18 to 30 cm; very dark greyish brown (10YR 3/2) sand; very weak coarse structure, held by very fine sand-binding roots; moist; medium and coarse clean quartz grains; common coarse, medium, and fine, and many very fine roots; clear smooth boundary.

EA—30 to 62 cm; light brownish grey (10YR 6/2) sand; very weak coarse structure held by very fine sand-binding roots; otherwise loose, single grain; moist; slightly cohesive; medium and coarse clean quartz grains; common coarse, medium, and fine, and many very fine roots; gradual smooth boundary.

E1—62 to 103 cm; light grey (10YR 7/1) sand; loose, single grain; subrounded, medium and coarse clean quartz grains; common coarse, and few medium, fine, and very fine roots; not cohesive, collapsing into pit from side walls and face; gradual smooth boundary.

E2—103 to 500+ cm; white (10YR 8/1) sand; loose, single grain; subrounded, medium and coarse clean quartz grains; very few medium, fine, and very fine roots to at least 300 cm.

Soil classification

Diagnostic horizons and features (Soil Taxonomy) are (*i*) xeric moisture regime, *(ii)* ochric epipedon from 0 to 30 cm, (*iii*) albic horizon from 30 to 500+ cm, (*iv*) >90% quartz sand in the particle-size control section, (*v*) <5% silt and clay in the particle size control section. The soil is an Entisol because it lacks diagnostic horizons in the upper 200 cm of the profile. The sandy particle size class places it in the Psamment suborder, and the dominance of quartz qualifies it as a Quartzipsamment at the Great Group level. The xeric moisture regime and lack of other diagnostic features qualifies the profile as a Xeric Quartzipsamment. In the absence of a spodic horizon (at least within the upper 5 m) the profile qualifies as an Arenic Grey-Orthic-Tenesol in the Australian Soil Classification System.

Physical and chemical properties

The soil consists of >97% sand with a bulk density between 1.3 and 1.5 g cm^{-3} (Appendix Table 1). The profile is therefore extremely well-drained, although the surface soil becomes water-repellent when dry. The sand is primarily medium and coarse grained (0.25 to 1.00 mm), although there is a greater proportion of fine sand below 340 cm (Appendix Table 2). The soil is moderately acid (measured in water). Total C and total N concentrations decline with depth, with wide C:N ratios (approximately 50–60; Table 3). The profile contains no carbonate, so total C is equivalent to organic C. Total P concentrations are extremely low throughout (<5 mg P kg^{-1}, and <3 g P m^{-2} in the upper metre of the profile), and corresponding C:P ratios exceed 6000 in the A horizon (Appendix Table 3). Exchangeable cations are low, particularly in the subsoil, and base saturation is 100% throughout (extractable Al, Fe, and Mn are undetectable; Appendix Table 4). Total mineral elements are very low, with undetectable concentrations of some micronutrients (i.e. B, Cu, Zn; Appendix Table 5).

DISCUSSION

That the soil is classified as a young undeveloped soil (i.e. an Entisol) despite its great age is an artifact of the US Soil Taxonomy system, which does not recognise old, coarse textured and strongly weathered soils such as the Bassendean, where diagnostic horizons are >200 cm deep. We did not encounter a spodic horizon in this profile, but if there was one at >5 m depth then the soil would qualify as a Giant Humosesquic Aeric Podosol in the Australian Soil Classification. Quartz-rich soils often contain insufficient metals to yield a spodic horizon and therefore develop into Quartzipsamments (Fanning & Fanning 1989). However, there are spodic horizons at depth in old Spearwood (Middle Pleistocene) and Bassendean dunes elsewhere on the Swan and Scott coastal plains. In addition, Giant Podosols are a feature of coastal dune chronosequences elsewhere in Australia, such as the Cooloola soil chronosequence in Queensland (Thompson 1981, 1992), albeit on younger (Middle Pleistocene) dunes than those studied here. Whether a spodic horizon lies at depth in the proposed Bassendean reference soil perhaps depends on water table depth, which has been linked to the presence of a spodic horizon elsewhere in the Swan Coastal Plain (McArthur & Russell 1978).

The Bassendean reference soil is extremely infertile, representing one of the most infertile soils worldwide. In particular, it contains an extremely small amount of total P, most of which is in organic form (Turner *et al*. 2018). Base cation concentrations are also extremely low, with cation exchange capacity almost entirely associated with soil organic matter. In these respects, the Bassendean reference soil is characteristic of Bassendean soils throughout the Swan coastal plain, with similar soils on the Scott Coastal Plain (e.g. near Warren Beach; Turner *et al*. 2018).

The sandy nature of the Bassendean soil means that it is extremely well-drained, although the surface soil can exhibit a high degree of water repellency when dry (Salama et al. 2005). This hydrophobicity is caused by coatings of waxy organic matter around sand grains (Roberts & Carbon 1972; Harper & Gilkes 1994) and is common in Western Australia (Roberts & Carbon 1971). Although the water-repellent surface soil can reduce infiltration, it appears to conserve soil moisture during the dry season by reducing evaporation (Rye

& Smettem 2017). Water-repellency can also be caused by fire (DeBano 1981), with subsequent surface runoff across the surface accelerating ecosystem retrogression by transferring ash and associated nutrients from dune crests to swales (Turner & Laliberté 2015).

The Bassendean soil is of considerable ecological and conservation importance in the region, because it supports a remarkable diversity of plant species, both taxonomically and functionally. Within the Swan Coastal Plain, both alpha and beta diversity reach their maximum values on the Bassendean dunes (Laliberté *et al*. 2014, Zemunik *et al*. 2016). Similarly, the diversity of plant nutrient-acquisition strategies is greatest on the Bassendean soil (Zemunik *et al*. 2015). Given that most of the extremely small concentrations of plant nutrients are associated with the surface soil, and that there are no subsoil nutrient reserves, the Bassendean soil is particularly sensitive to disturbance. It should have high conservation priority, especially considering that *Banksia* woodlands on Spearwood and Bassendean dunes around Perth are highly fragmented and threatened by urbanization (Ramalho *et al*. 2014; Department of the Environment and Energy 2016).

CONCLUSION

We present an alternative Bassendean reference soil for Western Australia. The new profile is located in an extensive area of Bassendean sand with undisturbed vegetation and a distinct dune morphology. The soil is extremely infertile and forms the end-point of the Guilderton soil chronosequence. These soils are extensive throughout the Swan Coastal Plain, with comparable soils under greater rainfall on the Scott Coastal Plain. The Bassendean soil has high conservation priority given its association with a threatened ecological community.

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APPENDIX.

Table 1
Bulk density and particle-sizes in genetic horizons of the proposed Bassendean reference soil. nd, not determined.

Depth cm	Designation	Bulk density (fine earth) g cm-3	Coarse fragments (>2 mm) % vol	Sand %	Silt %	Clay %	Textural class
0–1	A1	nd	0	99.3	0.1	0.7	Sand
1–18	A2	1.31	0	97.2	1.5	1.3	Sand
18–30	A3	1.46	0	98.6	0.7	0.6	Sand
30–62	EA	1.39	0	98.9	0.4	0.7	Sand
62–103	E1	1.36	0	98.9	0.4	0.6	Sand
103–340	E2 (1)	1.46	0	98.9	0.4	0.7	Sand
340–500+	E2 (2)	nd	0	99.3	0.1	0.7	Sand

Table 2
Sand size fractionation in genetic horizons of the proposed Bassendean reference soil.

Depth cm	Very fine sand (0.05–0.10 mm)	Fine sand (0.10–0.25 mm)	Medium sand (0.25–0.5 mm)	Coarse sand (0.50–1.0 mm)	Very coarse sand (1.0–2.0 mm)
	% total sand				
0–1	0.2	3.3	51.9	44.6	0.0
1–18	0.0	1.9	42.8	55.0	0.2
18–30	0.1	3.3	45.7	50.8	0.1
30–62	0.0	1.4	43.6	54.7	0.3
62–103	0.2	3.8	48.6	47.4	0.0
103–340	0.0	3.8	52.7	43.0	0.5
340–500+	1.1	28.1	52.3	18.4	0.0

Table 3
Soil pH and total carbon (C), nitrogen (N), and phosphorus (P) concentrations in genetic horizons of the proposed Bassendean reference soil.

Depth cm	Soil pH			Total C g kg^{-1}	Total N mg kg^{-1}	Total P[a] mg P kg^{-1}	C:N	C:P
	Water	$CaCl_2$	$BaCl_2$					
0–1	6.31	4.37	4.79	4.19	89.0	2.7	47.1	1534
1–18	5.94	3.80	3.63	28.98	594.5	4.6	48.7	6369
18–30	5.65	3.65	3.69	8.41	158.6	2.3	53.0	3613
30–62	5.55	3.64	4.08	2.78	45.2	1.7	61.4	1642
62–103	5.48	4.02	4.46	1.17	18.9	0.8	62.1	1447
103–340	5.61	4.42	4.84	0.34	3.6	1.0	94.5	358
340–500+	5.61	5.09	5.14	0.20	0.5	1.4	375.5	146

[a] Total P determined by ignition and acid digestion.

Table 4

Exchangeable cations by $BaCl_2$ extraction in genetic horizons of the proposed Bassendean reference soil. TEB, total exchangeable bases; ECEC, effective cation exchange capacity; BS, base saturation.

Depth cm	Al	Ca	Fe	K	Mg	Mn	Na	TEB	ECEC	BS %
	$cmol_c\ kg^{-1}$									
0–1	<0.01	0.40	<0.01	0.03	0.12	<0.01	0.02	0.58	0.58	100
1–18	<0.01	2.09	<0.01	0.03	0.54	<0.01	0.09	2.75	2.75	100
18–30	<0.01	0.79	<0.01	0.02	0.27	<0.01	0.03	1.11	1.11	100
30–62	<0.01	0.12	<0.01	0.02	0.05	<0.01	0.01	0.20	0.20	100
62–103	<0.01	<0.01	<0.01	0.02	0.01	<0.01	<0.01	0.04	0.04	100
103–340	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	0.01	0.01	100
340–500+	<0.01	<0.01	<0.01	0.02	<0.01	<0.01	0.01	0.04	0.04	100

Table 5

Total mineral elements determined by HNO_3 digestion in genetic horizons of the proposed Bassendean reference soil.

Depth cm	Al	B	Ca	Cu	Fe	K	Mg	Mn	Na	P	Zn
	$mg\ kg^{-1}$										
0–1	122	33	141	<1	43	17	28	<5	111	<5	<5
1–18	93	<5	549	<1	74	14	88	<5	25	<5	<5
18–30	24	<5	160	<1	33	<10	34	<5	17	<5	<5
30–62	13	<5	70	<1	58	<10	13	<5	9	<5	<5
62–103	13	<5	13	<1	93	<10	<10	<5	28	<5	<5
103–340	26	8	10	<1	123	<10	<10	5	17	<5	<5
340–500+	24	6	21	<1	226	14	<10	6	51	<5	<5

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Runoff and groundwater responses to climate change in South West Australia

DON MCFARLANE [1*], RICHARD GEORGE [2], JOHN RUPRECHT [3], STEVE CHARLES [4] & GEOFF HODGSON [4]

[1] *School of Agriculture and Environment, University of Western Australia, Perth, WA, Australia*

[2] *Department of Primary Industries and Regional Development, Bunbury, WA, Australia*

[3] *School of Energy, Water and Waste, Murdoch University, Perth, WA, Australia*

[4] *Land and Water, CSIRO Floreat Laboratories, Perth, WA, Australia*

[*] *Corresponding author:* ✉ *don.mcfarlane@outlook.com*

ABSTRACT

A warming and drying climate in the South West of Australia since about 1975, and especially from 2000, has reduced flooding and lessened salinisation risks, but also has reduced fresh water supplies. As well as continuous trends, there have been abrupt changes in hydrological processes as groundwater levels have receded from valleys.

In some cleared inland wheatbelt areas, saline groundwaters are still rising where the watertable is deep, clearing has been recent and/or the reduction in rainfall has been limited. Over time, groundwater level changes will better reflect the drying climate. The reduction in rainfall and higher potential evaporation rates has dried catchments overall, and greatly reduced runoff and major flooding, even in catchments where salinity is still expanding across valley floors. Major flooding after rare storms may occur, but now is more likely in summer than winter. It is now driven by infiltration-excess rather than saturation-excess runoff processes, depending on landscape position, and rainfall amount and duration. Episodic events, such as occurred in 2017, may increase salinity and flooding for a period despite the overall decreasing trend in such risks.

In the largely cleared Zone of Rejuvenated Drainage and vegetated Darling Range, groundwater levels in cleared areas are close to reaching a new equilibrium, with the drier climate reducing salinisation risks. In the largely forested Darling Range, groundwater levels are falling below stream beds thereby substantially reducing runoff into dams in the western part of the zone where groundwaters are fresh. As a result, Perth (population two million) has transitioned from being almost entirely dependent on such runoff for its drinking water, to not having any usable runoff in some years.

In the Perth Basin, groundwater levels are falling within sedimentary strata as the predominantly perennial vegetation uses a high proportion of incoming rainfall. The less intense and more intermittent rainfall is also increasing canopy interception and unsaturated-zone water losses. Cleared areas with high watertables are least affected because a reduction in recharge may be offset by less rejected runoff, lower drain flows and evaporation from vegetation tapping into groundwater. This buffering will continue until groundwater levels fall beneath drain inverts and plant rooting depths. The impact of the drying climate on groundwater levels has been masked to date by increasing recharge due to clearing and urbanisation. Streams connected to strata in the Perth and Collie basins usually gain fresher water from unconfined aquifers. With falling groundwater levels drainages are transitioning from gaining- to losing-streams, with reducing surface water flows and increasing risk of aquifer salinisation where the cross-cutting streams are saline.

Climate projections indicate a continuing drying trend is likely with increased temperatures and possibly a greater proportion of annual rainfall, and therefore flood risks, in summer. Water yields in dams and aquifers will continue to decline if these projections are correct. However, risks associated with too much water (salinisation, flooding, soil waterlogging) will probably continue to abate unless the amount and/or intensity of rainfall increases in the future.

KEYWORDS: Runoff, groundwater, recharge, climate change, salinity, Mediterranean climate, South West, Australia

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INTRODUCTION

The South West region of Australia (Fig. 1) is much wetter than expected for a west coast between latitudes 28° and 34°S. Deserts are common at similar locations in South America and southern Africa because of the cold, north-flowing Humboldt and Benguela currents, respectively, which flow up each coastline. The Indian Ocean has a similar anti-clockwise cold current flowing along the west coast of Australia, the West Australian Current, but its effect on rainfall is offset by the warm southerly flowing Leeuwin Current (Feng *et al*. 2003). This current arises from the alignment of islands in the Indonesian archipelago, and a difference in oceanic levels between the Pacific and Indian oceans. Because of the Leeuwin Current, annual rainfalls are 400 mm higher in the South West than for equivalent latitudes in the other two continents (Table 1).

Many areas around the world with a Mediterranean climate have experienced a hotter, drier climate in recent decades—a trend projected to increase and affect both water resources (Arnell 2004) and nature conservation values (Klausmeyer & Shaw 2009). Southwestern Australia has experienced a particularly abrupt and severe reduction in rainfall since about 1975 with this reduction being attributed, in part, to additional greenhouse gases (Hope *et al*. 2006; Cai & Cowan 2006; Frederiksen *et al*. 2017).

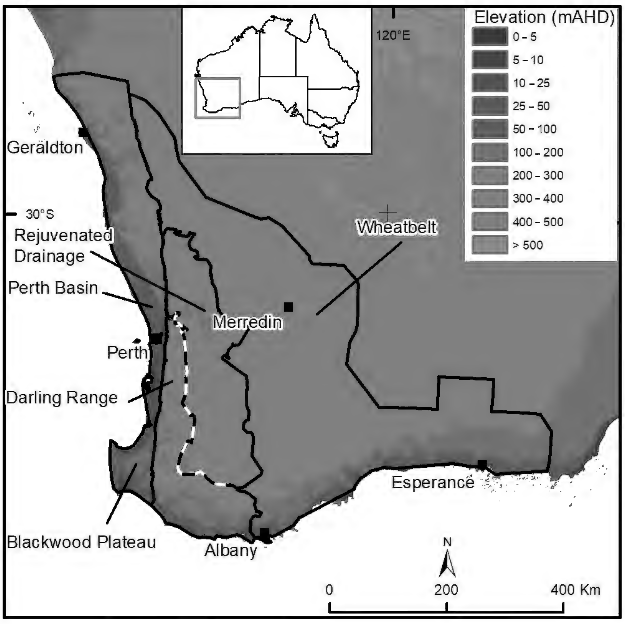

Figure 1. Location of Wheatbelt, Zone of Rejuvenated Drainage and Darling Range (separated by dashed line), and Perth Basin relative to topography in the South West, Western Australia. Background Landsat image from the National Aeronautics and Space Administration archive.

The region is unusual in that it has experienced little tectonic, glaciation or volcanic activity for hundreds of millions of years. As a result, it is flat, rivers are broad and ill-defined, weathering profiles are deep, and soils are infertile. This has allowed the accumulation of cyclic salts and, where native vegetation in inland areas was cleared, the rapid development of dryland salinity (Clarke *et al*. 2002). Shallow sand-over-clay (texture-contrast or duplex) soils are also common in inland areas. These profiles can fill with water and cause crops and pastures to be waterlogged in an otherwise water-limiting environment (McFarlane *et al*. 1992).

This paper examines the different impacts of this climate shift on the region's surface water and groundwater hydrology in the past four decades. It examines recorded trends in salinisation, flooding and water resource availability that are likely to intensify in the future. We also comment on what may happen if these trends continue, as have been largely correctly projected by Global Climate Models in the past 20 or more years.

PHYSIOGRAPHY OF THE SOUTH WEST

Both soil landscape and land cover affect how the hydrology of the South West has responded to the drying climate. For this overview, the area has been divided into three broad east-to-west regions, the Zone of Ancient Drainage (the cleared portion being the Wheatbelt), the Zone of Rejuvenated Drainage and the Perth Basin. The Zone of Rejuvenated Drainage has been sub-divided based on whether it has been largely cleared (in the east) or not (the Darling Range).

The Wheatbelt consists of a plateau covered by deeply weathered clay-rich profiles on Archaean granite and gneiss, over which native vegetation has been mostly cleared. Mulcahy & Bettenay (1972) called the larger region extending well beyond the Wheatbelt the 'Zone of Ancient Drainage'. Its valleys are wide and contain saline lakes and ephemeral rivers that predate progressive clearing in the last 175 years (Fig. 1). The regolith is often over 30 m deep and stores cyclic salts that have not been

Table 1. Comparison of annual average rainfall for areas on the west coasts of Australia, South America and Africa.

Western Australian location	Annual rainfall (mm)	South American location	Annual rainfall (mm)	South West African location	Annual rainfall (mm)
Geraldton 28°47'S	460	Vallenar 28°36'S	32	Alexander Bay 28°35'S	46
Lancelin 31°01'S	599	Coquimbo 29°57'S	106	Lambert Bay 31°40'S	140
Perth 31°96'S	868	Canela 31°23'S	170	Elands Bay 32°18'S	170
Bunbury 33°33'S	871	Valparaiso 33°10'S	462	Cape Town 33°55'S	515

leached over tens of thousands of years because of poor flushing (McFarlane & George 1992). Fresh water is limited in this region because of saline runoff and most groundwater salinities exceed 10 000 mg/L.

To the west of the Wheatbelt the regolith is thinner and the valleys more incised in the Zone of Rejuvenated Drainage (Mulcahy & Bettenay 1972) including the Darling Range sub-region. Whereas the soils are also clayey, especially below about 1 m, salt storage is less, and there are almost no saline lakes in the valleys.

The Darling Range has retained its cover of native forests whereas most of the Zone of Rejuvenated Drainage has been cleared for dryland agriculture (Fig. 2). Because of improved natural flushing, the western, higher-rainfall part of the Darling Range has lower salt storage in the regolith and groundwater is fresher than farther inland. Although groundwater salinities progressively increase to the east with reduced rainfall and flushing within the region, they are less than in the Wheatbelt. Consequently, forest clearing in the eastern parts can lead to increased stream salinities, whereas clearing in the higher-rainfall western part increases the runoff yield of fresh water.

The thick sedimentary succession in the Perth Basin is overlain by sandy soils and unconfined aquifers especially where there are sand dunes. The soils are mostly too permeable to generate sufficient runoff to develop defined drainage lines, except where the soils are clayey on the Blackwood Plateau and around floodplains where major inland drainages from the hinterland cross the basin and have deposited fine-grained material.

As salt storages are low, fresh groundwater is present in most coastal areas. Almost all the flat and low-lying Swan Coastal Plain along the westernmost part of the Perth Basin has been cleared of perennial vegetation, whereas elevated parts in the south (Blackwood Plateau) have retained their native vegetation (Fig. 2).

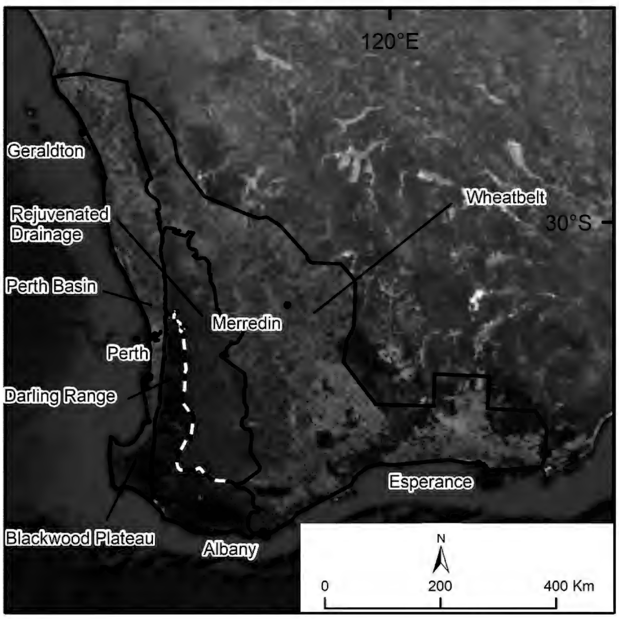

Figure 2. Land cover in the South West of Australia. Background Landsat image from Google Earth.

CLIMATE

The annual rainfall in the South West has reduced by 10–25% in its western parts since 1975 with a small area in the east and southeast recording an increase (Fig. 3). At first the decline in the western area was thought to be natural variability. It was not until the mid-1990s, when runoff into the dams that supply Perth became unreliable, that climate change was considered a factor (Bates *et al.* 2008, 2010).

Cool-season rainfall is far more effective than summer rain in generating runoff because evaporation rates are lower. Soils remain wetter for longer and profiles can become saturated leaving no room for further rain to infiltrate. Soils with sandy topsoils and clayey subsoils are common outside the Perth Basin. These 'duplex' soils are very effective in retaining water in their profiles because the sandy topsoil increases infiltration and decreases evaporative losses while the clay subsoil inhibits deep drainage. These soil types are therefore very susceptible to winter runoff and waterlogging. Figure 4 shows that cool season rainfall has decreased by 10 to 30% since 1975 over almost the entire South West.

Unlike eastern Australia, the South West is little influenced by the El Nino Southern Oscillation so the decline in rainfall has been progressive rather than punctuated by droughts followed by wet periods. This is shown in plots of normalised cumulative difference of mean (CDFM) annual rainfall for ten metrological stations across the South West (Fig. 5). Seven of the ten stations show periods of below average rainfall in recent decades. The year each decline started varies but the trends are clear. In contrast, rainfall at eastern stations (Lake Carmody, Welcome Downs and Codg Codgen) has been more consistent with a slight rising trend in recent years.

Although annual rainfall trends may vary, the proportion of rain falling in the wettest six months has shown a substantial decline at all stations except Cape Leeuwin in the South West (Fig. 6). The greatest declines have been at the three most eastern stations (Welcome Downs, Lake Carmody and Codg Codgen) where apparently more consistent total annual rainfall is due to increases in less-effective summer rain and decreasing winter rain.

Runoff is affected by the intensity as well as the amount of rainfall because soil infiltration rates can be exceeded (rainfall excess). Soils can also become saturated (saturation excess) after prolonged wet periods. Li *et al*. (2005) analysed daily rainfall for five stations in the Darling Range and Zone of Rejuvenated Drainage and found that post-1965 intensities were much lower. For example, in Manjimup (Darling Range sub-region) daily rainfalls with a 10% chance of being exceeded in any one year have reduced from about 78 to 40 mm. It is unclear how shorter duration rainfall events have changed, but rain comes more as showers interspersed with sun and wind rather than for extended periods (Hope *et al*. 2006). Under such conditions interception losses in tree canopies will be higher. The Bureau of Meteorology has also estimated that since 1975 daily temperatures in the South West have risen by about 0.5°C and pan evaporation by about 200 mm per annum (Bureau of Meteorology 2018).

In a water resource assessment using 15 Global Climate Models (GCMs) all projected less rainfall in the South West under three warming scenarios (Silberstein *et al.* 2012a). Under a Representative Concentration Pathway of 6.0 W/m^2, eight of 22 GCMs project no change in rainfall by 2040, ten project a decrease by 5–15% and four project a decrease of more than 15% (Climate Change in Australia 2018). A Representative Concentration Pathway (RCP) is the amount of radiative forcing produced by greenhouse gases in 2100. RPCs represent possible future emissions and concentration scenarios, with 6.0 W/m^2 being a mid-level of forcing. The decreases in winter and spring rainfall has a high confidence because of the agreement between GCMs (Hope *et al.* 2015). Therefore, decreased rainfall and increased temperatures and potential evaporation trends observed since the mid-1970s may continue in the future (Charles *et al.* 2010; IOCI 2012).

WHEATBELT AND ZONE OF REJUVENATED DRAINAGE

The accumulation of rainfall and dryfall salts, and lack of leaching from the deep clayey profiles in the Wheatbelt made it highly susceptible to dryland salination once deep-rooted native vegetation was replaced by annual crops and pastures. Surface outbreaks of salinity are greatly dependent on the time since clearing (i.e. the time needed to fill the unsaturated zones under valleys and hillslopes with shallow profiles), the frequency of wet years (especially in the 1950s and 1960s), and the annual rainfall zone (with low rainfall zones taking longer to fill).

By 2000 almost one million hectares (ha) of previously productive land was salt-affected to such an extent that it could not support non-halophytic plants (McFarlane *et al.* 2004). Land was being lost at a rate of about 14 000 ha per annum and an additional 2.8–4.5 million ha could be affected if watertables were to rise by a further 2 m above the valley floor area classified as being a salinity hazard. This extent was considered unlikely because of factors such as the drying climate (McFarlane *et al.* 2004). There were concerns that a four-fold increase in salt-affected land in valley floors could increase historic flood peaks by a similar amount (Hatton & Ruprecht 2001).

A network of groundwater monitoring bores established by the Western Australia Department of Agriculture (now the Department of Primary Industries and Regional Development) from the mid-1980s make it possible to determine how the drying climate mentioned in the previous section has affected recharge and discharge rates. About 700 bores across the South West

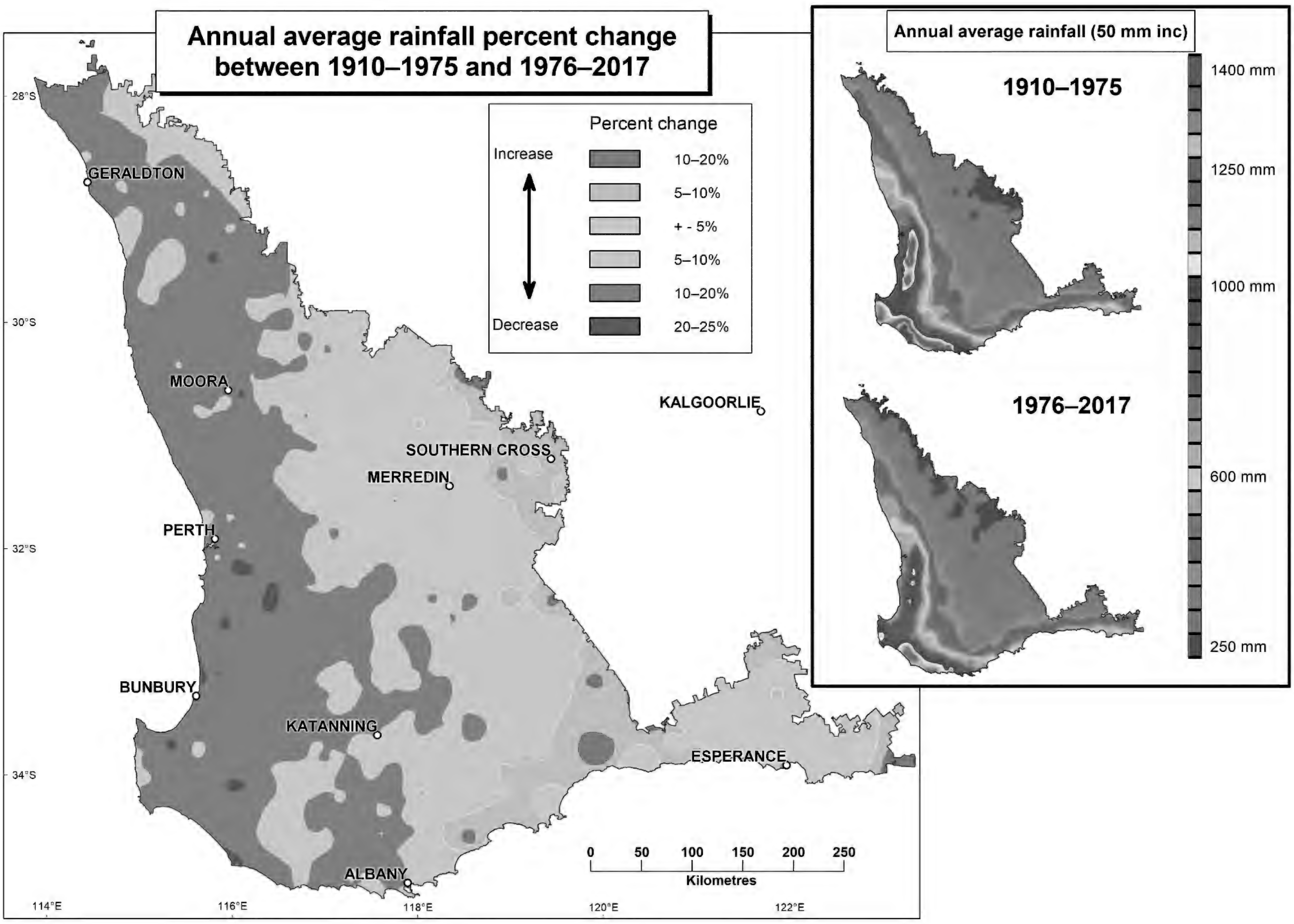

Figure 3. Average annual rainfall (upper right) and percentage change in annual average rainfall between 1910–1975 and 1976–2017 in southwestern Australia. Gridded data from Bureau of Meteorology and Department of Primary Industries and Regional Development weather stations.

have a sufficiently long record to estimate groundwater levels trends before and after 2000. The area with the highest proportion of salinity risk is near the South Coast (Fig. 7) because this region was cleared more recently and the decline in rainfall is less (Fig 3).

Two-thirds of all monitored bores had rising groundwater levels prior to 2000 but only 40% rose between 2000 and 2012 (Fig. 8). A quarter of all 700 bores were rising at a lower rate, indicating that the salt risk had decreased. Where watertables are deep it is possible that groundwater levels may never reach the surface especially if the climate continues to dry. Another satellite image monitoring survey is underway, which will assess whether the loss of 14 000 ha per annum to dryland salinity has continued or abated, along with continued monitoring of groundwater level trends to assess if the reduction in risk after 2000 is continuing.

Streamflows in the Wheatbelt and Zone of Rejuvenated Drainage have only been monitored since the 1970s. However, the annual exceedance probabilities (AEPs) of historic floods have been estimated from the extent of each flood within its floodplain or the height of flood waters on structures (Simon Rodgers, pers. comm. 2018). Using this record it is possible to plot AEPs against time for six major rivers in the South West (Fig. 9). Floods in the Swan, Murray and Greenough rivers were significantly higher in the past, indicated as lower AEP values ($P < 0.01$), than in recent decades. Floods in the Collie, Preston and Blackwood rivers have no significant trend ($P > 0.05$).

Maximum daily flows in the Swan River at Walyunga in 'winter' (April to September) and in 'summer' (October to March) show a decline in maximum flows in winter and a possible increase in the summer floods (Fig. 10a). These trends are also apparent in the Arthur River (a tributary of the Blackwood) at Mount Brown (Fig. 10b).

From the above observations, both historical flooding and maximum daily flows appear to be reducing in some rivers along with the decline in rainfalls shown in Figure 3. There is some indication that flood flows may be increasing in summer, which corresponds to the increased proportion of rain falling during this time of the year (Fig. 6). Increased wetting of the valleys because of rising groundwater levels therefore does not seem to be increasing flooding as has been predicted, with the lower rainfall (and possibly intensities), and higher temperatures and potential evaporation, being more important for runoff generation.

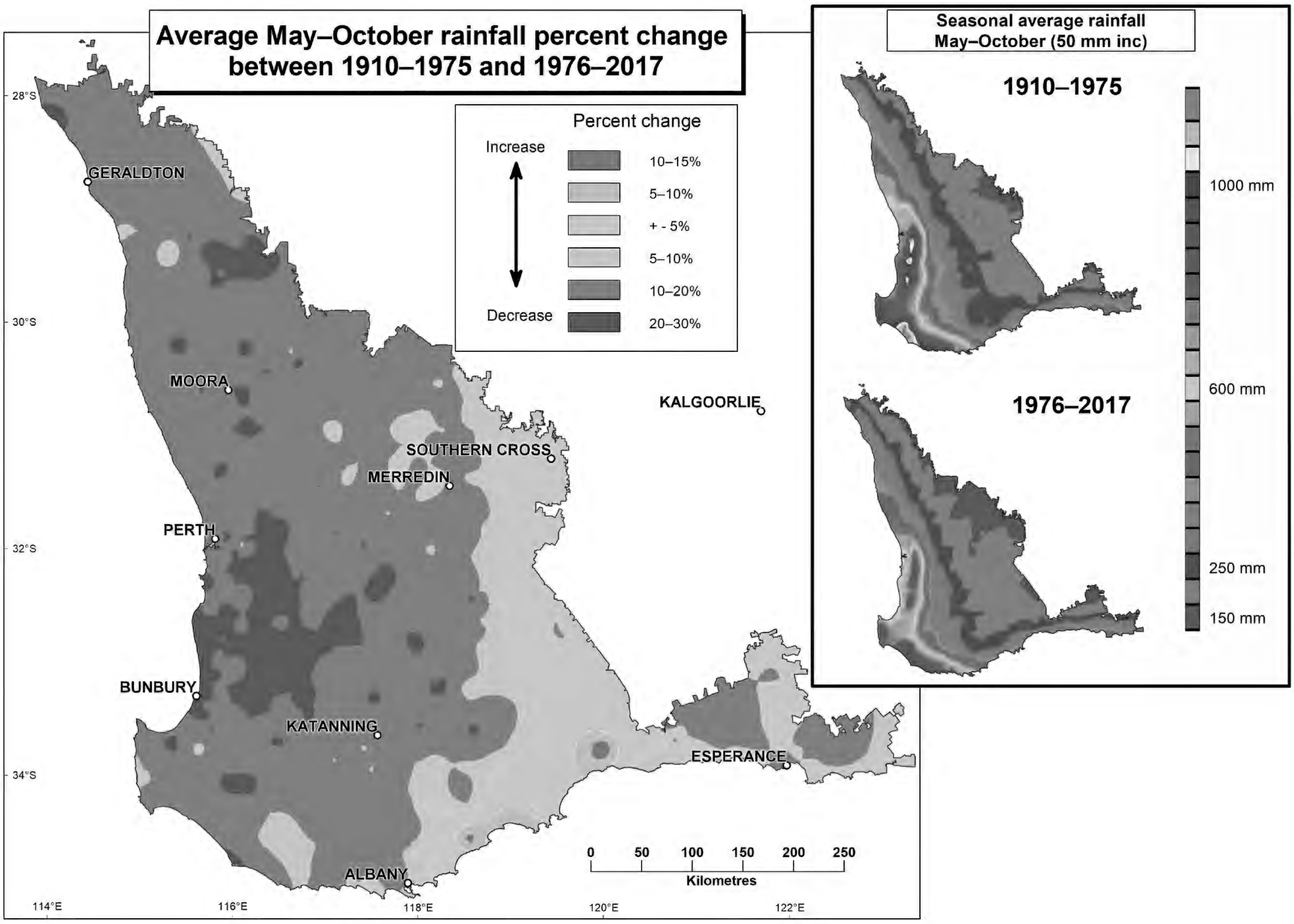

Figure 4. Average May to October rainfall (upper right) and percentage change in May to October rainfall between 1910–1975 and 1976–2017 in southwestern Australia. Gridded data from Bureau of Meteorology and Department of Primary Industries and Regional Development weather stations.

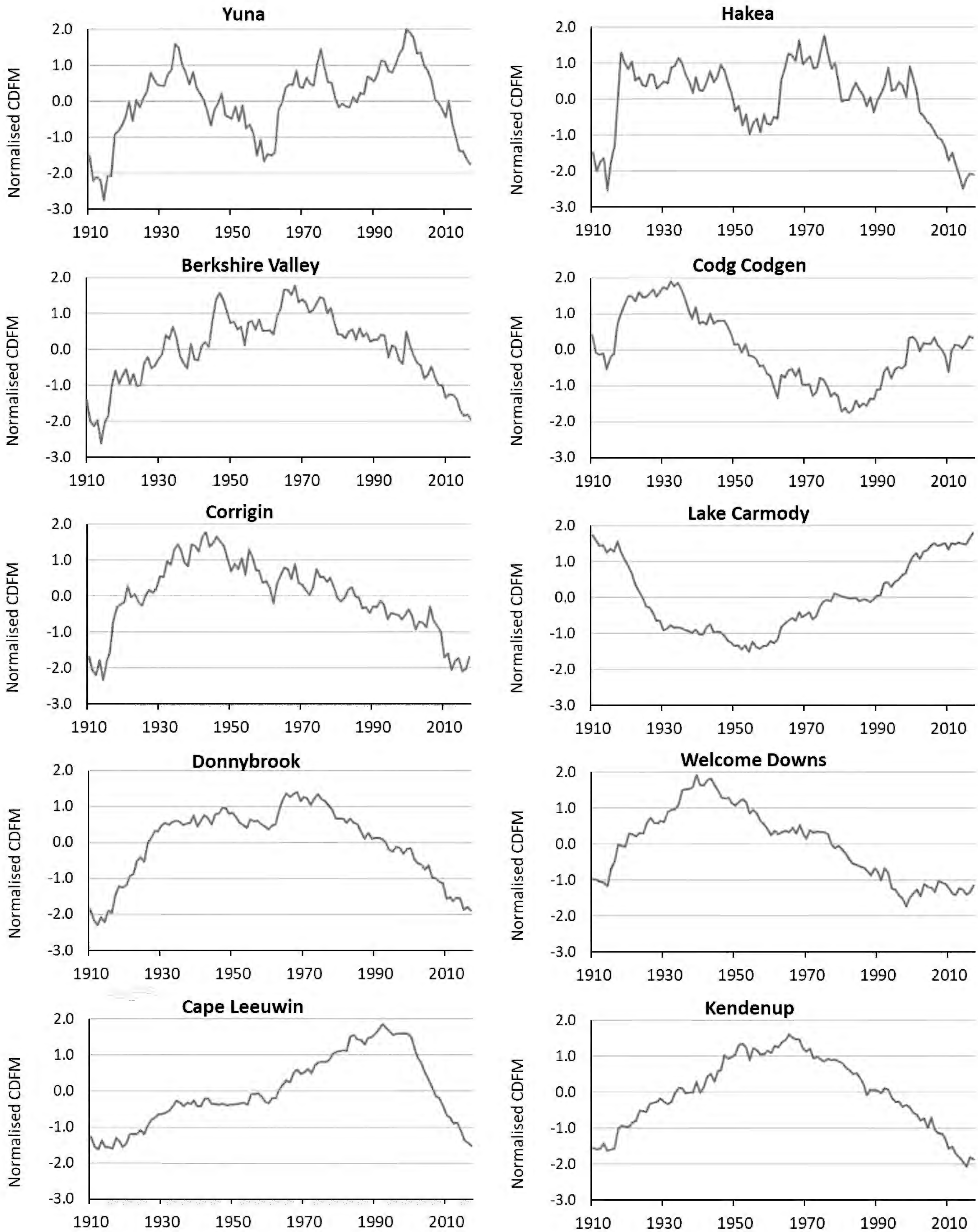

Figure 5. Changes in rainfall over the last ca. 100 years through normalised CDFM for 10 representative stations (Station locations shown in inset map along with the location of four catchments referred to later).

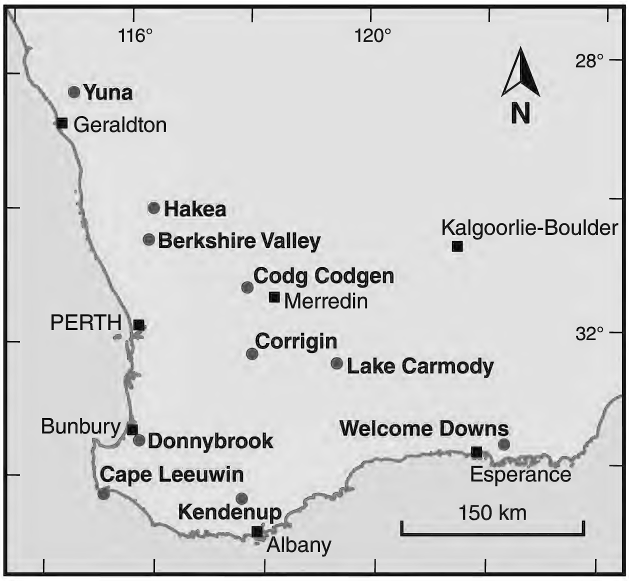

Figure 5. (Cont.)

In 1987 and 1988 about 60% of soils in an Upper Great Southern catchment had perched water in the root zone of crops and over 90% of the floodplain was waterlogged (McFarlane *et al.* 1992). Waterlogging and inundation (ponded surface water) were major constraints to cereal production before drier winters became more common. With the declining rainfall the Wheatbelt has therefore shifted to the southwest into what was termed the woolbelt (McFarlane & George 1994).

DARLING RANGE

Groundwater is a critical element for both streamflow generation and stream salinity in the Darling Range. The presence of a groundwater discharge area adds baseflow and provides a saturated zone for runoff generation (Ruprecht & Schofield 1991). Groundwater levels within forested research catchments in the Darling Range show a nearly continuous decline since 1975 (Kinal & Stoneman 2012; Croton *et al.* 2014). Trends for four catchments are shown in Figure 11. If the current trend in rainfall continues Croton *et al.* (2014) forecast that the regional groundwater in the Gordon research catchment could disappear by 2025.

Whereas groundwater levels are important because they respond to runs of dry years, shallow lateral throughflow in the upper gravelly sand horizon is the main source of streamflow in the jarrah forest in the Darling Range (Fig. 12). Williamson *et al.* (1987) calculated that in an above average rainfall year (1983), 90% of streamflow in a research catchment near Collie originated from throughflow. A perched watertable forms during winter in the sandy gravel or loamy surface soil above a relatively impermeable clay horizon (Stokes 1985; Ruprecht & Schofield 1991). Overland flow and groundwater discharge make minor contributions to annual flow volumes.

Stream salinity

Stream salinity is governed by the relative volumes and salinities of overland flow, shallow throughflow and runoff from valleys that have concentrated salts through evaporation over summer, and groundwater flow. Permanent groundwater, although a low contributor to total flow volume, is the major source of salts, but other flows tend to dilute this source.

Annual mean stream salinities of forested catchments range from 80 to 400 mg/L Total Dissolved Salts (TDS; Mayer *et al.* 2005). The lowest stream salinities (~ 100 mg/L TDS) are in low rainfall areas (mean annual rainfall less than 900 mm) where groundwater does not discharge into streams (Schofield & Ruprecht 1989). In high-rainfall areas (mean annual rainfall >1100 mm), where discharging groundwater salinities are low, stream salinities are again low (~150 mg/L TDS). Streams in the Intermediate Rainfall Zone (mean annual rainfall 900–1100 mm) have the highest salinities in all forest areas. Annual average values are commonly 250 mg/L TDS but can approach 400 mg/L TDS. These high salinities result from a limited discharge of groundwater of moderate salinity, combined with throughflow of low salinity (Loh *et al.* 1984).

Lower rainfall since the mid-1970s has not only reduced streamflows but also stream salinity for many forested streams (Fig. 13). This is probably due to lower groundwater levels along valleys preventing the discharge of higher salinity groundwater.

For any given salinity to streamflow relationship, a lower streamflow is likely to yield a higher salinity because the more saline groundwater contribution would remain relatively constant, but the fresher surface and shallow sub-surface runoff would be less. When valleys dry there is also less concentration of salts because of evapotranspiration.

Schofield & Ruprecht (1989) reported declining stream salinity in the Mt Saddleback catchments, whereas Kinal & Stoneman (2012) showed a reducing stream salinity over 1976–2011 for a forested research catchment. In both studies the reduction in salt load was greater than the reduction in streamflow, therefore the salinity concentration was lower for the period with lower streamflow.

It is therefore likely that stream salinity will continue to reduce in the fully forested catchments under the predicted climate change scenarios, albeit also with greatly reduced streamflows. The impacts of this reduction in salinity on stream ecology has not been considered in the literature. Some consequences could be the re-establishment of fresh-water species, although this is complicated with the significant reductions in streamflow volumes and in many cases dry streambeds for extended periods of time given the reductions in rainfall.

Runoff trends, rainfall–runoff relationships and non-stationary system

Ruprecht & Schofield (1989) identified the importance of groundwater discharge on streamflow generation after forest clearing. Bari *et al.* (1996) found a similar

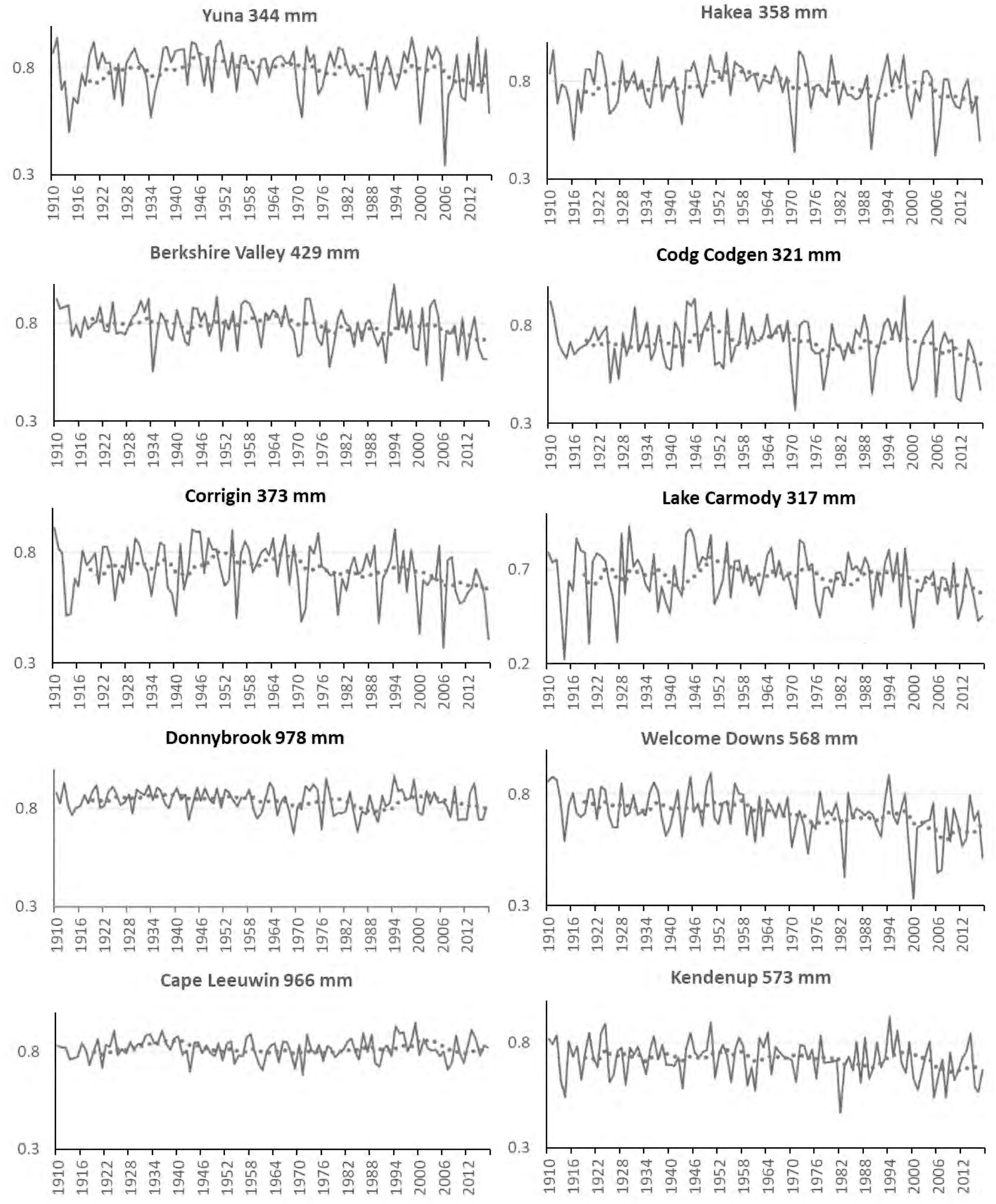

Figure 6. Proportion of annual rain that falls in the wettest six months (April–September for Codg Codgen, Hakea, Yuna, Corrigin and Lake Carmody; May–October for Berkshire Valley, Kendenup, Welcome Downs, Cape Leeuwin and Donnybrook) over time for ten South West rainfall stations. Moving average shown in red. Average annual rainfalls are in mm.

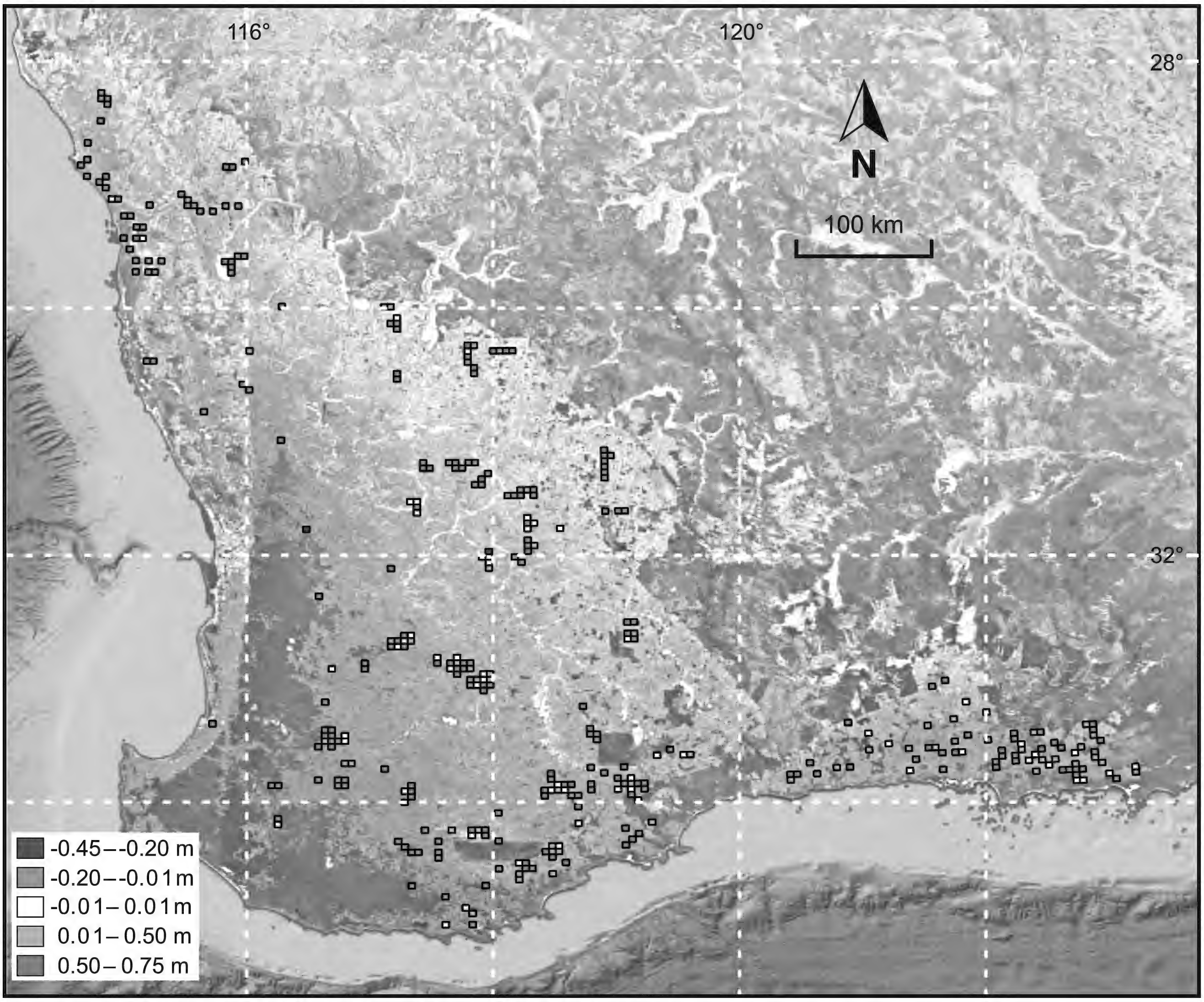

Figure 7. Change in groundwater trends (m/y) since 2000, each square is 5 x 5 km, the colour of the square is determined by the mean change in groundwater trend of the bores within the square since 2000. A blue square means the mean change in trend is positive (the groundwater is rising slower or dropping faster). A red square means the mean change in trend since 2000 is negative (the groundwater is rising faster or decreasing slower). Background image from Google Earth.

relationship with increasing water yield following timber harvesting in southern forests of the South West. Subsequent studies (Kinal & Stoneman 2012; Petrone *et al.* 2010) identified the influence of groundwater discharge areas on declining streamflows after rainfalls. Kinal & Stoneman (2012) found that for the Yarragil catchment in the intermediate rainfall zone of the Darling Range there was not only a change in the streamflow to rainfall relationship, but also greater variability. This change was also noted from drinking water supply catchments.

The importance of groundwater discharge areas on streamflow generation in the high-rainfall zone means that the drying climate has reduced streamflow more than expected for many catchments. The streamflow to rainfall relationship is, however, not consistent across the jarrah forest. The Salmon catchment (a fully forested research catchment in the Collie River catchment) does not show a change in relationship between rainfall and runoff. This is attributed to the lack of a significant groundwater discharge area contributing to streamflow generation, in this case estimated at only 1% of the catchment. Therefore, streamflow generation in the Salmon catchment is related to the 'wetting up' of the lower slope soil profile rather than being generated from a saturated groundwater discharge area.

The data from the water supply catchments supports the likelihood of a changing relationship between rainfall and streamflow (Fig. 14). The significance of the changing relationship is that for specific annual rainfalls the predicted annual streamflow has decreased substantially since 2001. This relationship may continue to change or it may represent a new equilibrium relationship.

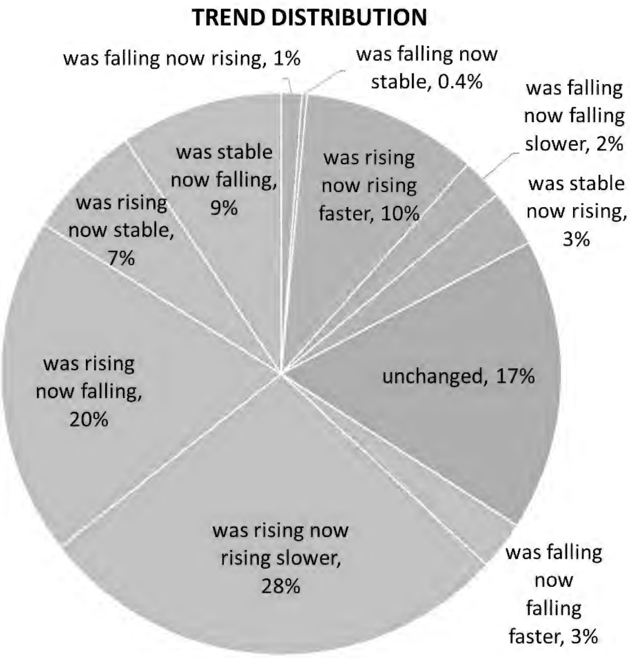

Figure 8. Trends in groundwater levels in 700 bores in southwestern Australia comparing before 2000 and 2000–2012.

The reduction (based on total volume) in mean annual streamflow from 1975–2000 compared to 2000–2012 was 51% while mean annual rainfall only declined by 9%. From the linear regression 30% of the contribution to the reduction in streamflow is attributable to the change in mean annual rainfall, and 70% is from the change in the rainfall to runoff relationship.

Silberstein *et al.* (2012a) indicated that the median future climate rainfall may decline by another 10%. Based on the existing rainfall to runoff relationship this equates to a further runoff decline of 30%. Petrone *et al.* (2010) considered "rainfall variability superimposed on falling watertables as an important cause of streamflow decline in SWWA [the South West] observed as a threshold response in a changing climate". In addition the changes in flow duration and monthly flow distribution for forest streams can be related to falling groundwater levels and loss of groundwater-surface water connectivity, contributing to lower annual runoff (Petrone *et al.* 2010). The observed current declines in catchment runoff and Perth water reservoir inflows brings into question the reliability of surface water catchments for future water supplies as well as the ecology of jarrah forest streams (Petrone *et al.* 2010).

While rainfall in higher rainfall areas has continued to decline by 6–7% since 2000, streamflow at the water supply catchment scale has declined by 45–55%. One explanation for the decline is that a lag in the groundwater response to the lower rainfall since 1975 has delayed changes to the rainfall to streamflow relationship. Alternatively, the changing approach to jarrah forest management (Conservation Commission of Western Australia 2013) over the last 30–40 years may be a contributing factor to the declining water yields (Burrows *et al.* 2011).

Water availability within the forest is considered a key driver of vegetation patterns and the types and abundance of fauna. Watertables in the northern jarrah forest have fallen by approximately 0.2 m/y over the last 35 years (Croton *et al.* 2012; Kinal & Stoneman 2012) and streamflow has reduced by more than 50% over the same period. This has resulted in many streams becoming ephemeral, more variable and less frequent flows, and projections that more streams will become ephemeral. The impact of the changes to the forest river hydrology on the aquatic ecology is not well understood but is likely to be significant.

Water yield into Perth reservoirs

The decline in water inflows into southwestern reservoirs is 28–58% for urban water supplies and 18–42% for irrigation water supplies (Fig. 15). Over all sources the total mean annual flow has reduced from 435 to 265 GL/y, or by 39%. In addition to the reduction in mean annual flow, streamflows have become more variable with the average coefficients of variation increasing from 0.42 to 0.55.

The drying climate in the South West has not only reduced streamflows but has impacted on the forest environment. Although ecosystems such as the jarrah forest are understood to be resilient to drought and other disturbances, Matusick *et al.* (2013) observed a sudden and unparalleled forest collapse in small parts of the jarrah forest corresponding with record dry and heat conditions in 2010–2011.

In the section on Climate we showed how rainfall is projected to decrease whereas temperatures and potential evaporation are expected to increase. Previous modelling studies at the large water supply catchment scale found that for a unit change in rainfall there was a threefold change in runoff (Berti *et al.* 2004; Kitsios *et al.* 2009; Silberstein *et al.* 2012a; Smith *et al.* 2009). However, the data from the water supply catchments (Fig. 16) indicates that this change may be greater than that.

Silberstein *et al.* (2012a) estimated the impact of climate change on the main water supply catchments in 2030 under scenarios in which rainfall declined by 2% (wet), 8% (median) and 14% (dry) compared to the average between 1975 and 2007 using 15 Global Circulation Models (GCMs). This analysis projected a change in mean annual inflow from -7% for the wet scenario to -43% for the dry scenario. However, over 2001–2013 the inflow into these reservoirs has averaged 94.5 GL, which represents a reduction of 36%, i.e. close to the dry scenario. This may mean that the climate impacts on inflow to major water supply reservoirs for Perth have been under predicted.

PERTH BASIN

The decline in annual and seasonal rainfall since 1975 has been most marked in the west across the Perth Basin (Figs. 3, 4). Nevertheless, recharge has been enhanced across this region due to clearing of native vegetation and highly permeable sandy soils.

The watertable is less than 10 m deep over about half of the Perth Basin south of Moora (185 km north of Perth) and less than 3 m across most of the Swan Coastal Plain

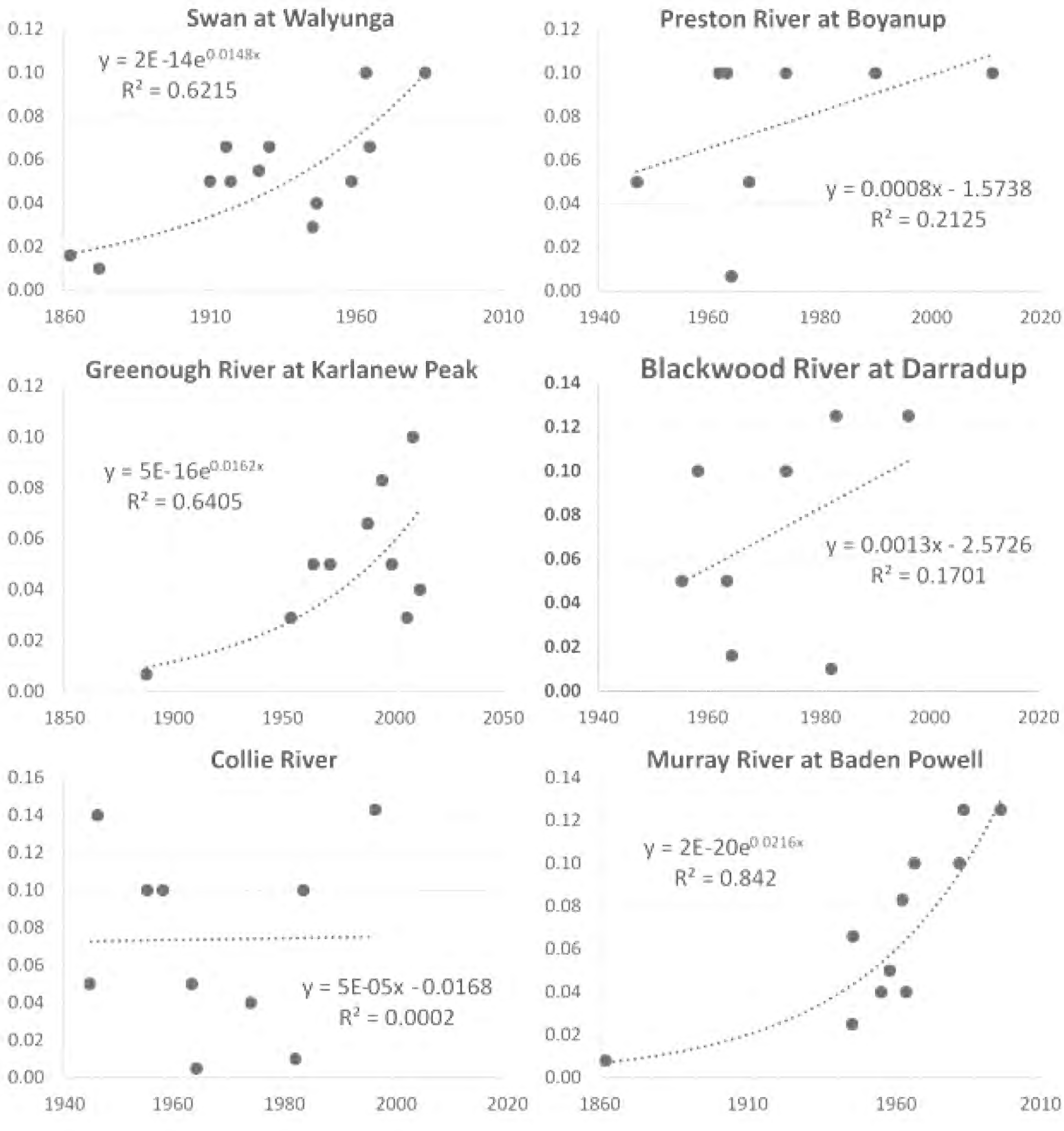

Figure 9. Annual exceedance probabilities of floods for six South West rivers. Data from Department of Water and Environmental Regulation.

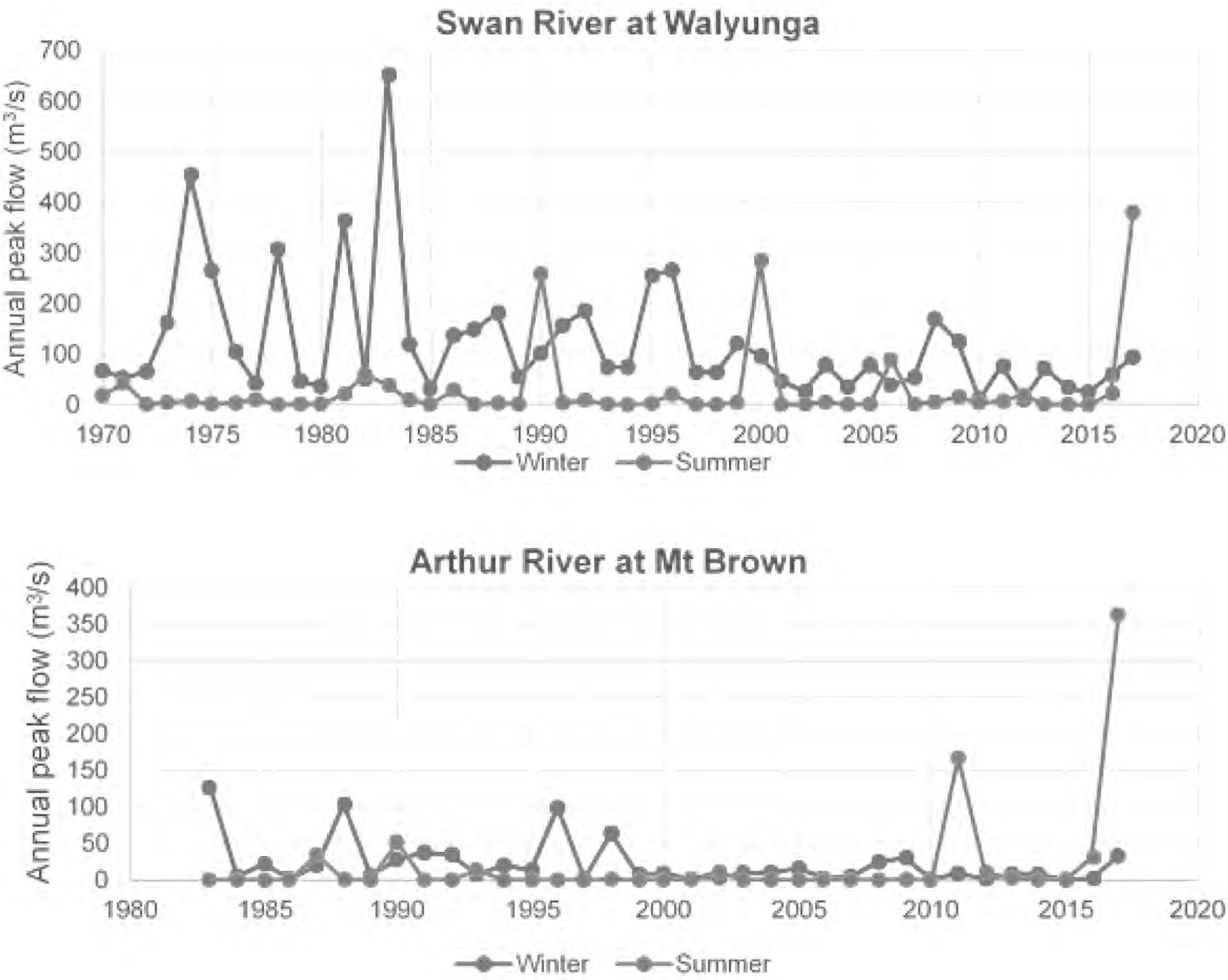

Figure 10. Maximum winter and summer flows in a) the Swan River at Walyunga; and b) the Arthur River at Mt Brown. Data from Department of Water and Environmental Regulation.

(Barron *et al*. 2012). Where watertables are close to the surface, there are losses because of direct evaporation from wetlands, uptake by vegetation that can access the watertable, and by drains used to remove water to enable agriculture and urbanisation. Researchers have shown that native and introduced vegetation (e.g. pines) can access the watertable when it is within 15–18 m of the surface (McFarlane 1984; Silberstein 2012b).

Maps of watertable changes for 2000–2015 show significant falls in unconfined groundwater levels in the south, while a few have risen (Fig. 17). The distribution of monitored bores reflects the intensity of use of the aquifer with it being heavily used on the Swan Coastal Plain around Perth and Peel, and less used where the watertable is much deeper in the north and under the mainly forested Blackwood Plateau in the south. The greatest recorded falls are north of Perth in the Gnangara Mound area and south of Perth near the eastern edge of the coastal plain. Gnangara has one of the most extensive covers of Banksia woodland left on the Swan Coastal Plain, pine plantations and pumping for both public and private use, all of which have impacted on groundwater levels (McFarlane *et al*. 2012).

Where the watertable is close to the surface, buffering (as described above) can reduce falls to 1 m or less, despite the decline in rainfall over 35 years. It is only when winter recharge fails to replace the losses over summer that the watertable starts to accumulate losses and falls of over 5 m are recorded. Groundwater-throughflow wetlands on the Swan Coastal Plain are usually less than 2 m deep so many have dried because of the fall in groundwater levels (Barron *et al.* 2012). Falls have been greatest under perennial vegetation as would be expected given interception by both the canopy and root systems.

The impact of climate on groundwater levels is evident in Figure 18. Landuse (except pine removal) and pumping were kept constant for four climate scenarios applied to three regional groundwater models for the Perth Basin south of Moora (Ali *et al*. 2012). For all the

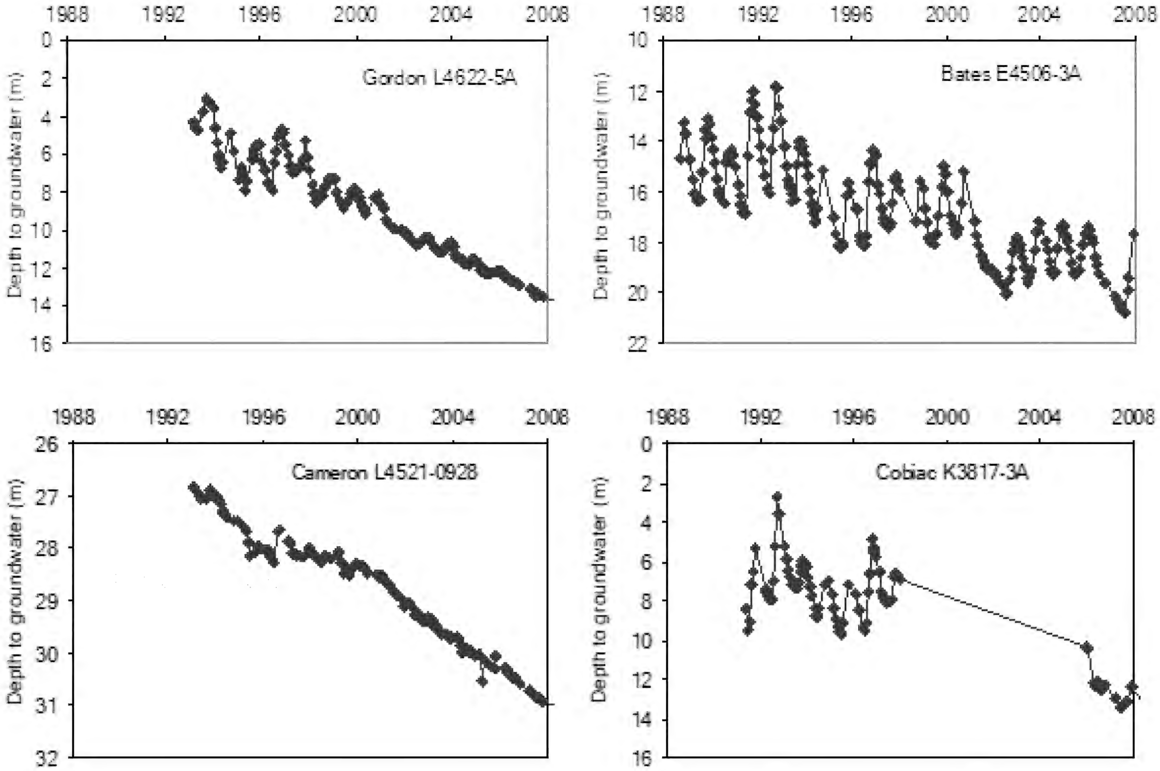

Figure 11. Groundwater levels declines in four Darling Range catchments (CSIRO 2009a). Bates, Gordon and Cameron are in the Murray basin, and Cobiac is a sub-catchment of the Wungong Brook.

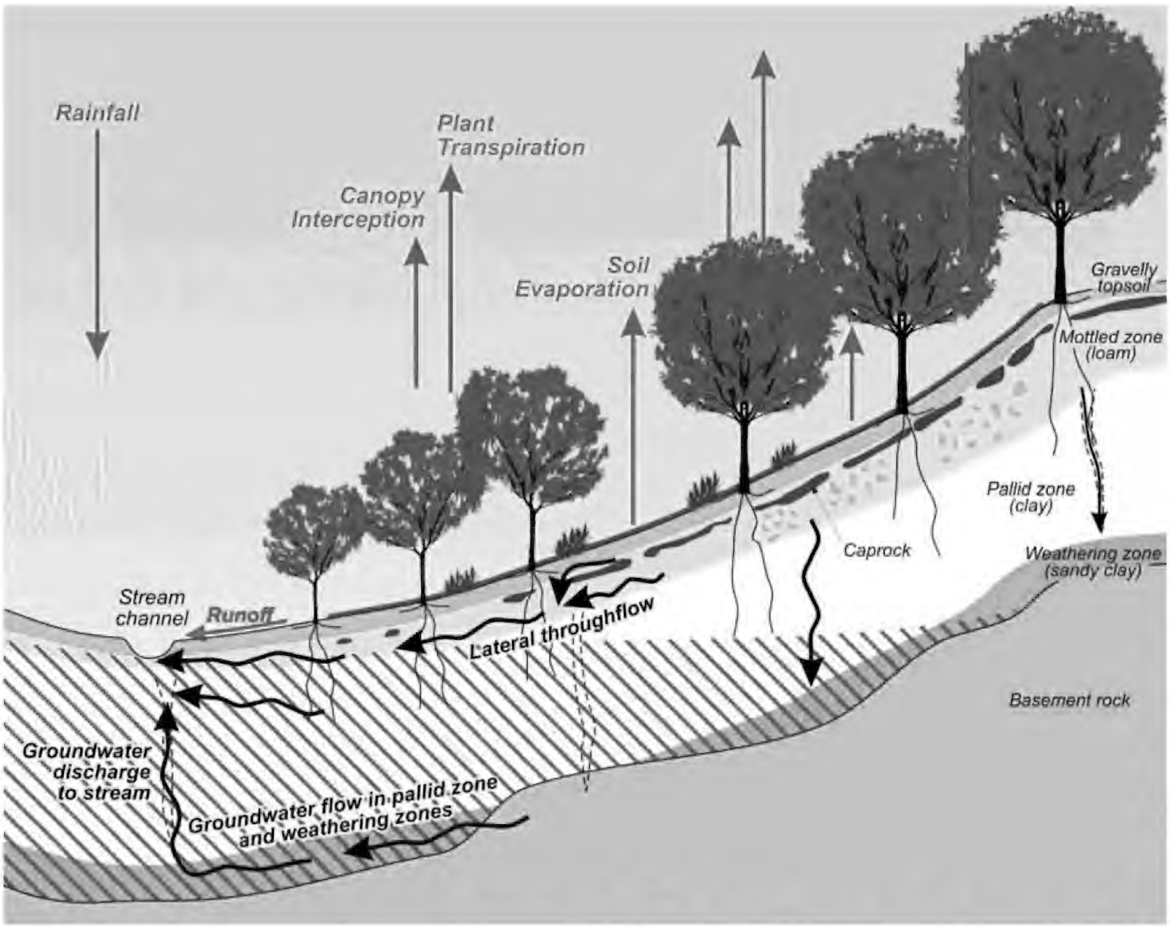

Figure 12. Cross-section showing typical Darling Range valley and runoff processes (CSIRO 2009a, fig. 3-3).

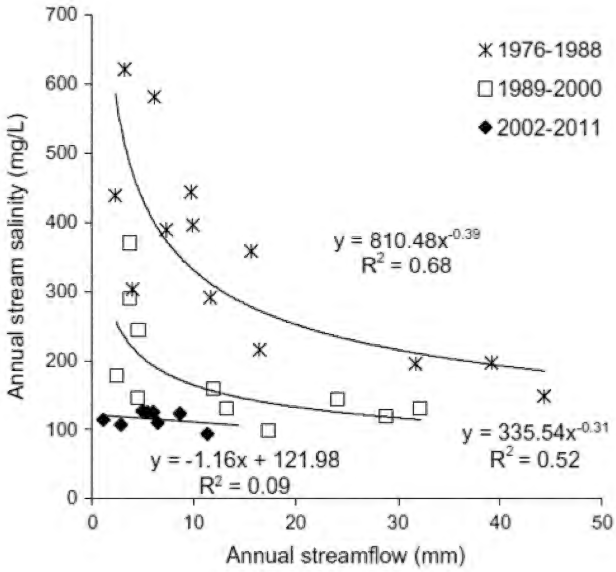

Figure 13. Flow-weighted annual stream salinity to annual streamflow relationship for 1976–1988, 1989–2000 and 2002–2011 (Kinal & Stoneman 2012).

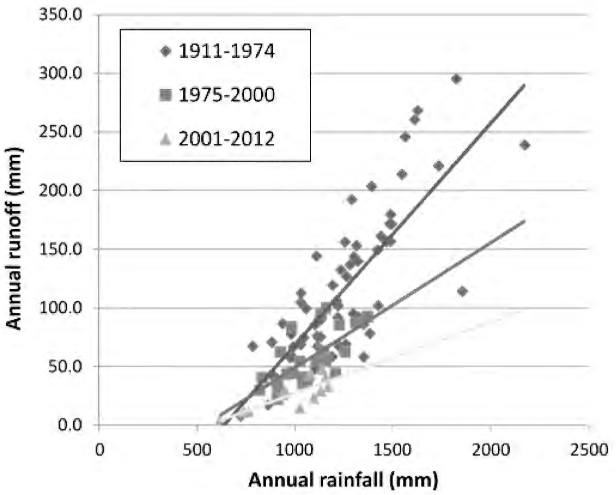

Figure 14. Changes in rainfall–runoff relationship over time in a typical catchment (Serpentine River).

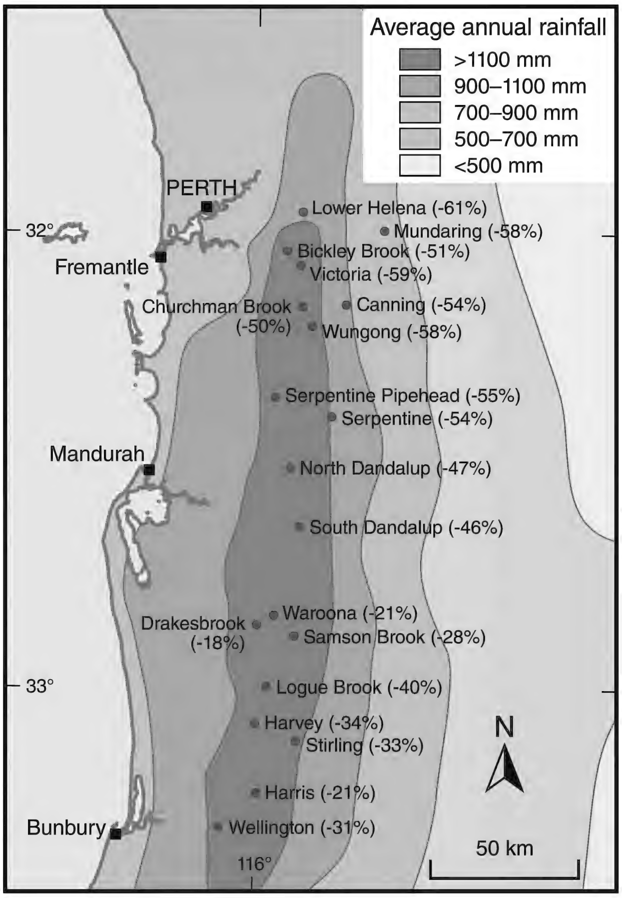

Figure 15. Percentage decrease in runoff in Darling Range catchments for 2001–2012 compared with 1975–2000. Data from Water Corporation.

resultant climate scenarios groundwater levels across the Blackwood Plateau and the Gnangara Mound fell because of vegetation. Climate scenarios in Figure 18 become drier from left to right. Perennial vegetation is anticipated to use an increasing proportion of the lower rainfall, thereby reducing recharge. Modelling of recharge showed that there was a one- to three-fold change in recharge for a unit change in rainfall for all combinations of soil, cover and climate examined (Dawes *et al*. 2012). This sensitivity to rainfall is also evident in runoff in the Darling Range (Silberstein *et al*. 2012a).

In an area west of the Gnangara Mound groundwater levels were projected to rise after pines were removed. The largely cleared Swan Coastal Plain is less affected by the drying climate because, as mentioned above, reduced rainfall initially causes less surface water drainage and evapotranspiration losses rather than lower groundwater levels. This is a form of 'rejected recharge'. Once storages in the aquifer at the end of summer are not replenished by winter recharge, levels start to fall as shown in the Dry Scenario.

Across the Dandaragan Plateau water levels are projected to rise because it is largely cleared, the soils are permeable, rainfall is moderate (500–600mm per annum) and there is limited extraction. This is comparable to inland wheatbelt areas that experience dryland salinity. However, in this case the groundwater is mainly fresh, and wetlands form in low-lying areas.

Given the highly permeable soils across the Perth Basin, the few streams that originate within it are the result of groundwater discharge. Falls in streamflow therefore reflect reductions in groundwater level. Rivers that cross the Perth Basin usually gain fresh baseflow from the unconfined superficial aquifer. However, as groundwater levels fall, these rivers may become losing streams and those that are saline may contaminate the aquifer (CSIRO 2009b). Therefore, the relative impacts of a drying climate on runoff and groundwater levels needs to be understood to predict whether past hydrological processes will continue or reverse.

The modelling results in Figure 18 were developed using three regional groundwater models calibrated using rainfall and groundwater level data from the wetter 1975–2007 years. Observed groundwater level changes between 2000 and 2015 in Figure 17 show that the model projections were optimistic. Levels have been following the Future Dry scenario that only has a 10% probability of being exceeded.

DISCUSSION AND RECOMMENDATIONS FOR FURTHER WORK

Changes induced by the poleward movement of the climate system that bring most of the winter rain to Australia's South West are similar in Mediterranean climate zones around the world. The South West is unusual in having a higher rainfall than other west coasts in the southern hemisphere because of the warm Leeuwin Current. The long-term topographic stability of the region (unaffected by glaciation, volcanism or substantial uplift for several hundred million years), has produced poor drainage and a deep regolith in which rainfall and dryfall salts have accumulated. The progressive clearing of perennial vegetation in the past 180 years has altered the water balance and mobilised some of the salt stored in the Wheatbelt and Zone of Rejuvenated Drainage.

The drying and warming climate that has been most evident since 1975, and especially after 2000, must be understood in this broad context. Runoff was the first hydrological change to be observed after dams used for metropolitan drinking water supplies failed to meet demands. The reduction in flooding of inland areas and the gradual drying of throughflow lakes on the Swan Coastal Plain have been less well reported. All these reductions in surface hydrology were preceded by falls in groundwater levels, which was detected because there has generally been good monitoring of aquifers across the region. In Darling Range catchments, aquifers have been monitored since the 1980s because of concerns that the clearing of native forests for bauxite mining could cause stream salinisation. Similarly, groundwater levels over large areas in the Wheatbelt were monitored to assess salinisation risks, and levels in the superficial aquifer around production borefields across the Perth Basin were monitored after the *Environmental Protection Act 1986* required that lakes with high conservation values be protected.

Both runoff and recharge reduce about three-times for a unit reduction in rainfall. This relationship is affected by landuse and how close the watertable is to the surface. When watertables are high there can be rejected recharge because there is insufficient room for the incoming water. This is the case over large parts of the Swan Coastal Plain where the reducing rainfalls have not (yet) affected groundwater and lake levels for many years. The relationship is also affected when watertables fall below the invert of streams in the Darling Range, reducing both saturation-excess runoff and baseflow. This resulted in stepped reductions in runoff as rainfall–runoff processes changed, which points to the development of a non-stationary hydrological system.

The effect of landuse on reductions in runoff and recharge as the climate changed is more complex. Perennial vegetation is expected to transition to more

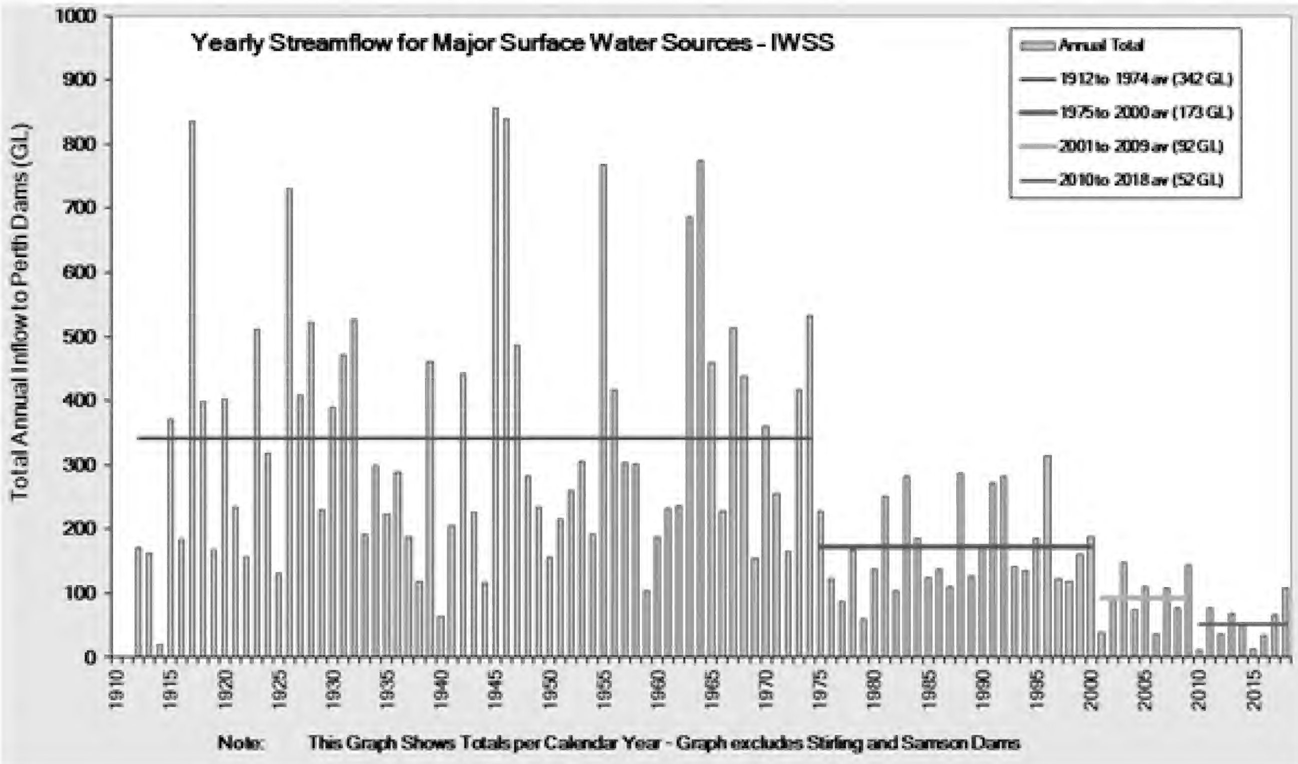

Figure 16. Trends in runoff into Perth metropolitan reservoirs supplying drinking water to the Integrated Water Supply Scheme or IWSS. Data from Water Corporation.

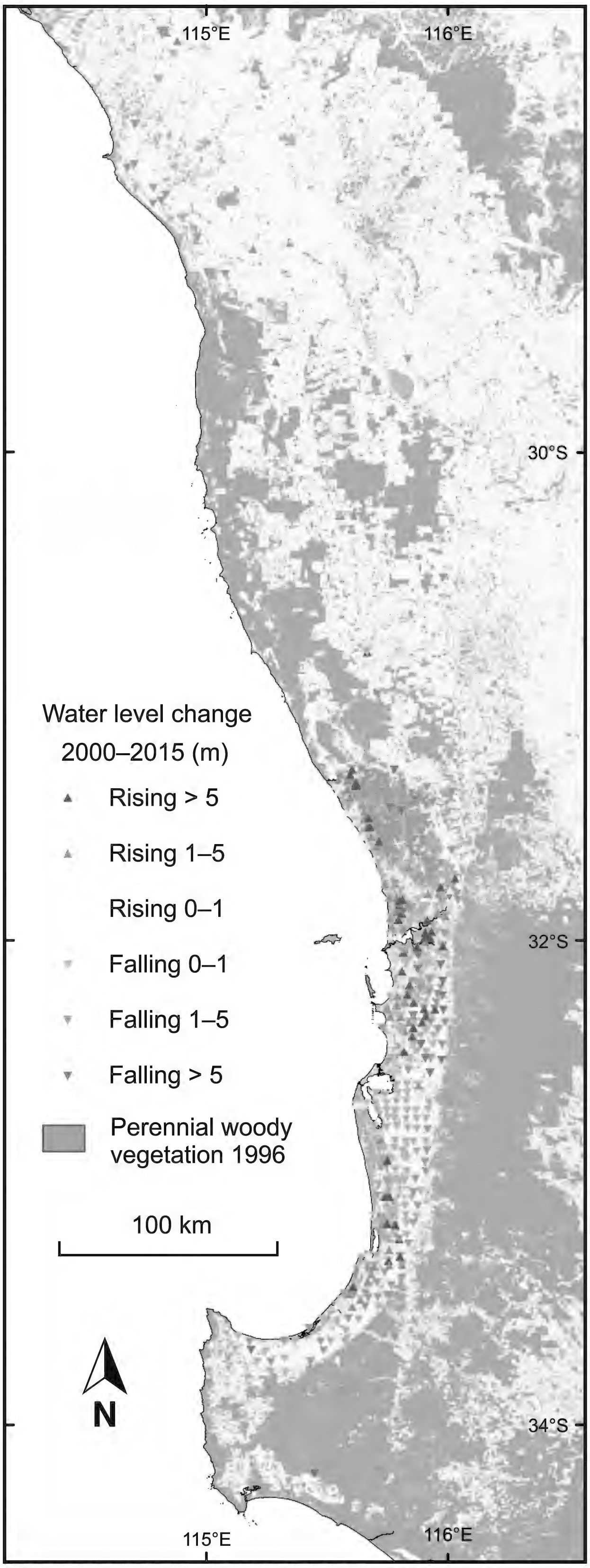

Figure 17. Changes in groundwater levels on the Perth Basin between 2000 and 2015 in relation to perennial vegetation. Data from Department of Water and Environmental Regulation & Department of Primary Industries and Regional Development.

xeric communities under a hotter and drier climate. However, perennial vegetation has already started to thicken and expand as a result of CO_2 fertilisation (Donohue *et al.* 2013). In the South West these factors have probably encouraged vegetation to use a higher proportion of incoming rainfall. There are inadequate data to identify these processes, and there may be thresholds beyond which the vegetation cannot adapt quickly enough, i.e. such adaptation may be non-linear. For example, the widespread death of native trees in the Darling Range (especially on shallow soils) were reported after a very dry year in 2010 and a following hot-dry summer (Matusik *et al.* 2013). The authors concluded that Mediterranean-type forests, once thought to be resilient to climate change, may be susceptible to sudden and severe forest collapse when key thresholds have been reached. Urban areas are increasingly covering parts of the Swan Coastal Plain as native vegetation is cleared. Increasing urban density can at least partially offset the effects of lower rainfall and higher temperatures on the water balance because runoff from man-made surfaces are mostly directed into the superficial aquifer (McFarlane 1984).

The hydrology of the Wheatbelt is responding to climate change in complex ways depending on the time since clearing, the depth of the regolith and the degree of climate change, all of which are geographically determined. Groundwater systems are variably equilibrating with the recent climate where clearing was early, annual rainfalls are higher, and/or where the regolith is shallow. Overall it appears that the hotter, drier climate is reducing the risk of flooding, salinisation and waterlogging. However, dryland salinity is still increasing in some areas and long lags in groundwater response suggest it will remain a problem for decades. It is probable that the rate of salinity spread of 14 000 ha/y for 1989–1997 has now reduced because of the drying phase since 2000; however, this cannot be confirmed without repeated acquisition of data. Episodic events, such as occurred in 2017, may increase salinity and flooding for a period despite the overall decreasing trend in such risks. Whether summer rainfall will become a more significant driver of flooding and salinisation remains to be seen.

Comparisons between the South West of Australia and other Mediterranean regions to climate change would allow the anticipation of changes and sharing of response of adaptation practices. Understanding the causes for the reduction of runoff into Perth metropolitan dams has shown that they are unreliable future water sources. This has resulted in more confident investments in new borefields, seawater desalination and reuse, including indirect potable reuse of treated wastewater.

A reassessment of salt-affected areas is underway for the South West to see if rates have decreased as foreshadowed by the groundwater trends. Maintaining these monitoring systems to track responses, and to define risks and opportunities, is critical for the next decades. Understanding how native and introduced vegetation is adapting to an altered hydrology due to land use and climate change will enable better management of both conservation and forestry estates.

Climate change impacts on hydrology have caused some benefits (reduced flooding, waterlogging and

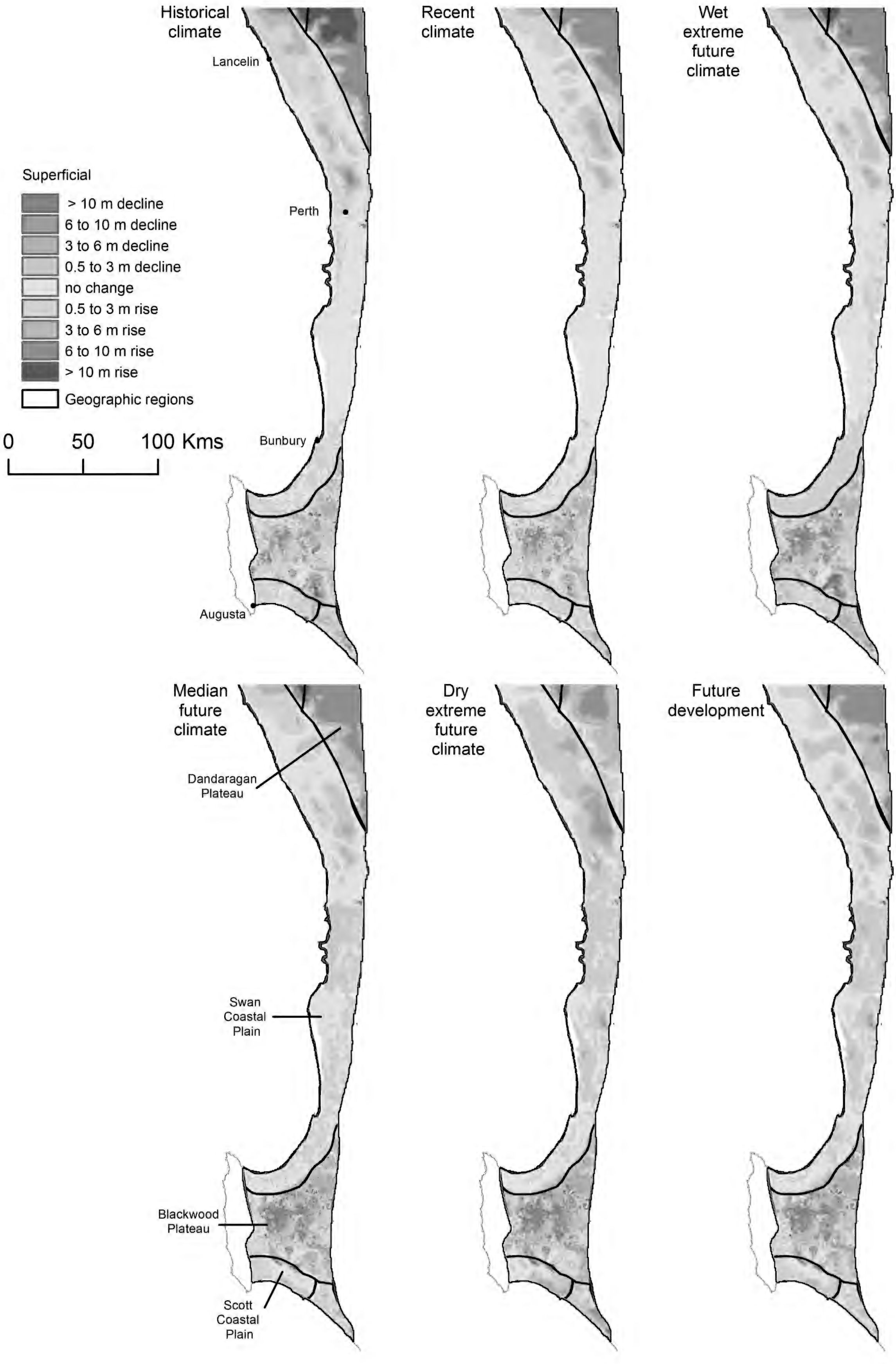

Figure 18. Projected changes in groundwater levels under four future climate regimes showing a) a continuation of the 1975–2007 climate, b) a continuation of the drier 1998–2007 climate, c) an even drier median future climate from Global Climate Models and d) a dry future climate from Global Climate Models (from Ali *et al.* 2012).

salinisation risk) but exacerbated problems (reduced water resources and impacts on native vegetation, riverine ecology and wetland systems). The assessment and conclusion in this paper are heavily dependent on effective monitoring without which an understanding of trends and changes in hydrological processes will not be apparent. This understanding is critical to enable effective resource management decisions now and in the future.

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New perspectives on Western Australian seagrass and macroalgal biogeography

DIANA WALKER [1 *], JOHN M HUISMAN [2], KIERYN KILMINSTER [1,3] & JOHN KUO [4]

[1] *School of Biological Sciences, University of Western Australia, 35 Stirling Highway, Perth, WA 6009, Australia*

[2] *Western Australian Herbarium, Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, 17 Dick Perry Avenue Kensington, Locked Bag 104, Bentley Delivery Centre, WA 6983, Australia*

[3] *Department of Water and Environmental Regulation, WA Government, Locked Bag 10 Joondalup DC, WA 6919, Australia*

[4] *Research Infrastructure Centres, University of Western Australia, 35 Stirling Highway, Perth, WA 6009, Australia*

* *Corresponding author:* ✉ *diatom@iinet.net.au*

Abstract

The widespread adoption of new methodologies, especially molecular techniques, has dramatically changed our understanding of how species of seagrasses and macroalgae are classified and distributed. One consequence of this new paradigm is increased uncertainty regarding biogeographic studies based on pre-molecular species records. The question "how does one delineate an individual species?" has changed and differing interpretations may alter how previous assessments are viewed. In some instances, specimens previously regarded as a single species have been shown to represent multiple genetic lineages. An extreme example is that of the red alga *Portiera hornemannii*, now thought to include 21 cryptic species in the Philippines alone, and possibly up to 96 species in the wider Indo-Pacific. Reworking and reclassification of species based on DNA analyses have sunk many species into one, or combined or reorganized genera. These changes in taxonomic concepts have implications for conservation and biogeographical assessments, but our understanding of many groups is still in its infancy and requires further work. In order to address these mounting challenges, significant investment and a commitment to taxonomic research will be required in the coming decades.

Keywords: seagrass, macroalgae, taxonomy, biogeography, molecular sequencing

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INTRODUCTION

Seagrasses and macroalgae are important marine primary producers that provide significant structural habitat in coastal waters (Walker & Bellgrove 2017; Bellgrove *et al.* 2018), and support diverse faunal communities (van der Heide *et al.* 2012). Western Australia is well-known as a centre of biodiversity for seaweeds and seagrasses, with numerous species recorded and a particularly high percentage of endemic taxa. Several recent publications have included detailed descriptions of the state's marine flora (seagrasses in Larkum *et al.* 2018; macroalgae in Huisman 2015, 2018) and this paper does not reiterate those works. Rather, we will describe the history of marine plant biodiversity knowledge in Western Australia, then discuss how new methodologies, especially molecular techniques, have made dramatic changes to our understanding of how species of seagrasses and macroalgae are classified and distributed. The implications of these changes may be significant, with real impacts on marine biodiversity assessments, and potential impacts on environmental legislation.

SEAGRASSES

Western Australian waters are rich in seagrass species, both in diversity and areal extent. The history of seagrass collectors and collections are summarised in Figure 1. The state's 26 currently recognized seagrass species represent almost 40% of the world's approximately 70+ known species (Kilminster *et al.* 2018; Larkum *et al*. 2018; Waycott *et al.* 2014), a concentrated diversity not found in any other region. Western Australian seagrasses are widely distributed across coastal areas and estuaries (Carruthers *et al.* 2007) and a variety of habitats, although they are most commonly found associated with shallow, sandy substrata. Most of the Western Australia's temperate species are endemic, while those occurring in tropical waters are more widely distributed across the Indo-Pacific region. A list of currently recognised species across all of the Western Australian coast (Table 1) is divided into three major regions (South West, South-Coast, and Tropical WA) with dominant species life history strategies (colonising, opportunistic or persistent, sensu Kilminster *et al.* 2015) also indicated.

The published patterns of distribution and biogeography have changed little from the earlier historical records summarised in Walker (1991). The historical and present-day drivers shaping biogeography patterns are explored and distributional changes due to

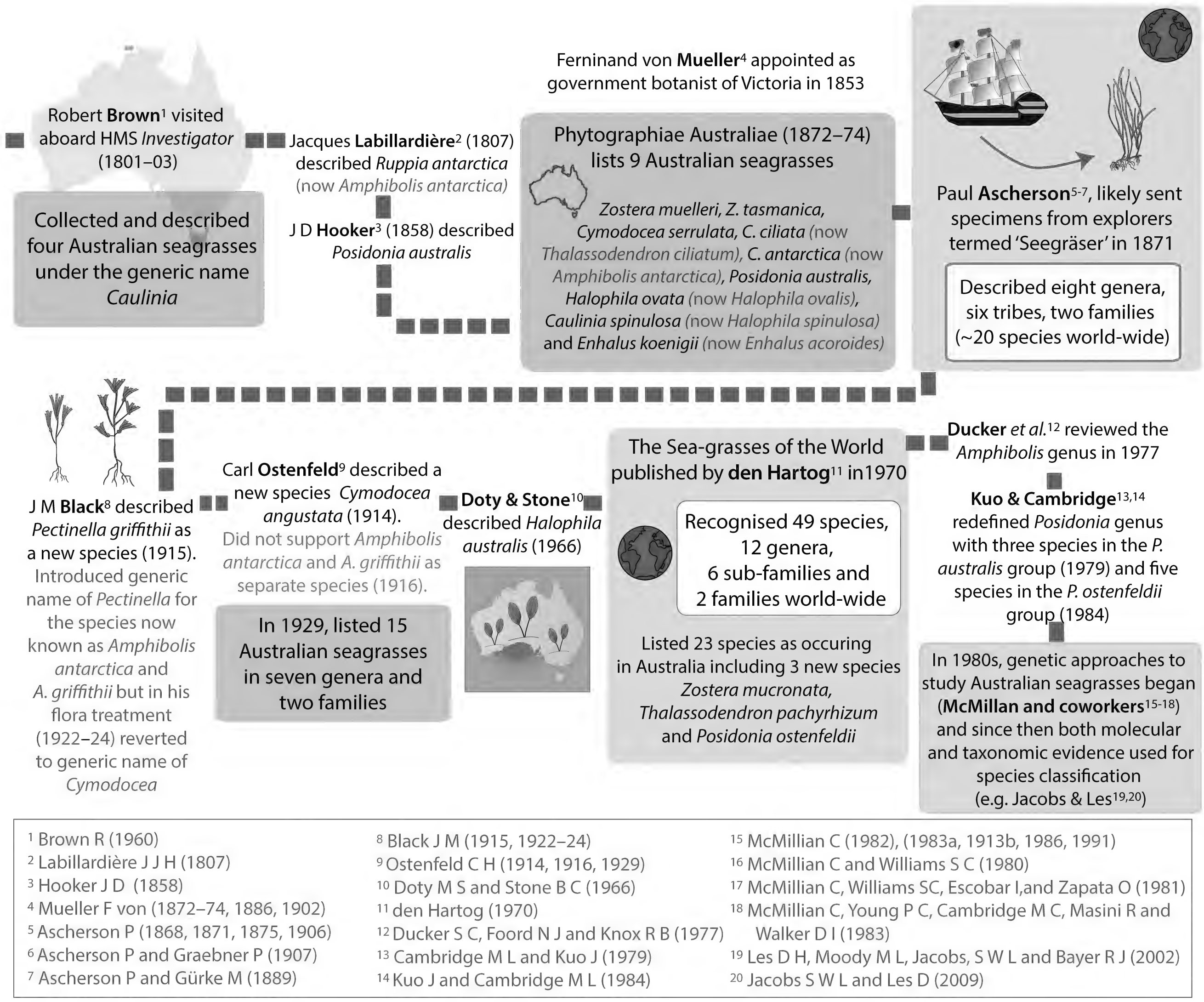

Figure 1. A selection of notable botanists and their contributions to Australian seagrass knowledge from 1800–2010.

anthropogenic and climate impacts for the south-west of Western Australia are reported in Kilminster *et al.* (2018).

Recent seagrass research in Western Australia has primarily focused on ecophysiological aspects or studies of recruitment and population structure. Many of the ecophysiological studies have shifted in focus to the roots and rhizomes of seagrasses, specifically exploring relationships between sediment biogeochemistry, seagrass health and the microbes that inhabit the seagrass rhizosphere (Fraser *et al.* 2017; Kilminster *et al.* 2014; Martin *et al.* 2019; Martin *et al.* 2018; Olsen *et al.* 2018). A conservation and restoration agenda has driven the studies of recruitment and population structure, with enhanced understanding of the potential of seed-based restoration, recruitment-bottlenecks and genetic connectivity between populations (Kendrick *et al.* 2017; McMahon *et al.* 2017; McMahon *et al.* 2018; Sinclair *et al.* 2018; Statton *et al.* 2017a; Statton *et al.* 2017b). Most of these areas of new knowledge were initiated in response to the broad-scale threat that climate-change and extreme events pose in the region; e.g. the wide-scale losses of the seagrass in Shark Bay as a response to the 2011 marine heatwave (Ariaz-Ortiz *et al.* 2018; Kilminster *et al.* 2018). It is likely that climate-driven changes will alter the biogeography of seagrasses in the region in decades to come.

Over the last decade, 10 new species have been added to the Australian seagrass flora (Larkum *et al.* 2018), but several of these are reclassifications of existing records and their validity is the subject of much debate (Waycott *et al.* 2018). Kuo (2005) found that *Heterozostera* was not a monotypic genus but consisted of at least three Australian species. He redefined *H. tasmanica* and described two new species, *H. nigricaulis* J. Kuo and *H. polychlamys* J. Kuo, in the process removing *H. tasmanica* from the Western Australia flora. Jacobs & Les (2009) formally rejected *Heterozostera* as a genus and transferred the two new described *Heterozostera* species into the genus *Zostera* as *Zostera nigricaulis* (Kuo) S.W.L Jacobs & Les and *Zostera polychlamys* (Kuo) S.W.L Jacobs & Les.

Molecular studies (Les *et al.* 1997) appeared to support the recognition of only one genus instead of two

Table 1

Seagrass species list by three major Western Australian regions indicating dominant species life history. Small symbols indicate the species exhibit cross-over traits whereas the large symbols indicate the dominant life form.

Australian Region	Genus	Species	Species life history C	O	P
Southwest					
19 species total	*Amphibolis*	*A. antarctica*		◆	⬩
		A. griffitthi		◆	⬩
	Halodule	*H. uninervis*	◆	⬩	
	Syringodium	*S. isoetifolium*		◆	
	Thalassodendron	*T. pachyrhizum*			◆
	Posidonia	*P. angustifolia*			◆
		P. australis			◆
		P. sinuosa			◆
		P. ostenfeldii		⬩	◆
		P. coriacea			◆
		P. denhartogii			◆
		P. kirkmanii			◆
		P. robertsoniae			◆
	Halophila	*H. australis*	◆		
		H. decipiens	◆		
		H. ovalis	◆		
	Zostera/	*Z. muelleri*	⬩	◆	
	Heterozostera	*H. nigricaulis*	⬩	◆	
		H. polychlamus	⬩	◆	
South Coast					
17 species total	*Amphibolis*	*A. antarctica*		◆	⬩
		A. griffitthi		◆	⬩
	Thalassodendron	*T. pachyrhizum*			◆
	Posidonia	*P. angustifolia*			◆
		P. australis			◆
		P. sinuosa			◆
		P. ostenfeldii			◆
		P. coriacea		⬩	◆
		P. denhartogii			◆
		P. kirkmanii			◆
		P. robertsoniae			◆
	Halophila	*H. australis*	◆		
		H. decipiens	◆		
		H. ovalis	◆		
	Zostera/	*Z. muelleri*	⬩	◆	
	Heterozostera	*H. nigricaulis*	⬩	◆	
		H. polychlamus	⬩	◆	
Tropical					
10 species total	*Cymodocea*	*C. serrulata*		◆	
		C. rotundata		◆	
	Halodule	*H. uninervis*	◆	⬩	
	Syringodium	*S. isoetifolium*		◆	
	Thalassodendron	*T. ciliatum*			◆
	Enhalus	*E. acoroides*			◆
	Halophila	*H. ovalis*	◆		
		H. decipiens	◆		
		H. spinulosa	◆		
	Thalassia	*T. hemprichii*			◆

Notes: Information within this table is derived from Kilminster *et al*. (2015, supp. table 1), Kilminster *et al*. (2018) and IUCN Redlist website (www.iucnredlist.org)

Southwest = Shark Bay to Cape Leeuwin, South-Coast = Cape Leeuwin to Great Australia Bight, Tropical is north of Shark Bay to the Northern Territory border.

Dominant life history: C = colonising, O = opportunistic and P = persistent (sensu Kilminster *et al.* 2015).

genera in the Australian Zosteraceae. However, other taxonomists who focused primarily on morphological characteristics (Den Hartog & Kuo 2006; Kuo 2011) retained both genera, *Heterozostera* and *Zostera*.

Agreement on how many species of seagrass exist has proved elusive. There is currently significant disagreement between species lists described using morphological traits (Kuo *et al.* 2018) and those derived from molecular studies (Coyer *et al*. 2013; Les *et al.* 2002; Waycott *et al.* 2018). Seagrasses are notably plastic in their morphological characteristics; in particular, attributes such as leaf width and leaf thickness can vary dramatically with environmental conditions, a testament to their ability to adapt to a variety of underwater environments. This plasticity may present challenges for identifying species with traditional taxonomy (although species differentiation by reproductive traits has generally proved stable with both taxonomic and molecular agreement). With the recent use of molecular tools for examining seagrass populations, and indeed studies sequencing whole genomes (Lee *et al.* 2016, 2018), it is anticipated that significant progress will soon be made towards resolving these controversies.

MACROALGAE

As is probably true of most marine taxa, knowledge of the diversity and distribution of the Western Australian macroalgae has historically accumulated erratically, with major advances primarily associated with individual collectors and taxonomists (Fig. 2). Some of the earliest algal specimens were collected by Archibald Menzies in 1791 on HMS Discovery and later by Robert Brown, who was the botanist accompanying Mathew Flinders during 1801–03 on HMS Investigator. Dawson Turner described these algae, all from King George Sound, but the collections included only five species. The first resident collector was Johann August Ludwig Preiss, who lived in the Swan River colony from December 1838 to January 1842, making a large collection that included about 3000–4000 species, from an area extending from about 100 km north of Perth south to Albany and east to the vicinity of Cape Riche. Sonder (1845, 1846–1848) described more than 80 new species of algae based on the Preiss specimens, but unfortunately the precise collection localities were deemed unnecessary and only 'occidentales Novae Hollandiae' [Western Australia] was given. Undoubtedly, the phycologist with the greatest impact historically was the Irish botanist William Henry Harvey, who visited Australia in 1854–1855, arriving in Western Australia where he made collections from the Fremantle region and the south-west coast, before moving to Victoria, Tasmania and New South Wales. Harvey was a fervent collector, amassing a staggering 20 000 specimens during his 18 months in Australia. Womersley (1984) calculated that on many days he must have collected and prepared well over 100 specimens, and Harvey reported from King George Sound "In one day I collected and preserved 700 specimens, some being new kinds." Harvey's Western Australian collections were described primarily in a paper written 'at sea', en route to Victoria (Harvey 1855).

Following Harvey, documentation of the Western Australian marine flora essentially languished for over a century, at which time the South Australian phycologist H.B.S (Bryan) Womersley embarked on a life-long study to document the marine flora of southern Australia, a region that nominally extended to Cape Naturaliste in south-west Western Australia, but also included species records from further north. Womersley's studies culminated in the six volume series 'The Marine Benthic Flora of Southern Australia' (Womersley 1984, 1987, 1994, 1996, 1998, 2003), undoubtedly one of the most significant contributions to documenting Australia's algal diversity. Western Australia was also visited by phycologists from other parts of Australia (e.g. Gerry Kraft, Bill Woelkerling), but it was not until late in the 1980s that resident phycologists (JMH & DIW) began making significant contributions to macroalgal biodiversity assessments for Western Australia.

The focus of Harvey, Womersley and most visitors has been the southern and central coasts, leaving the

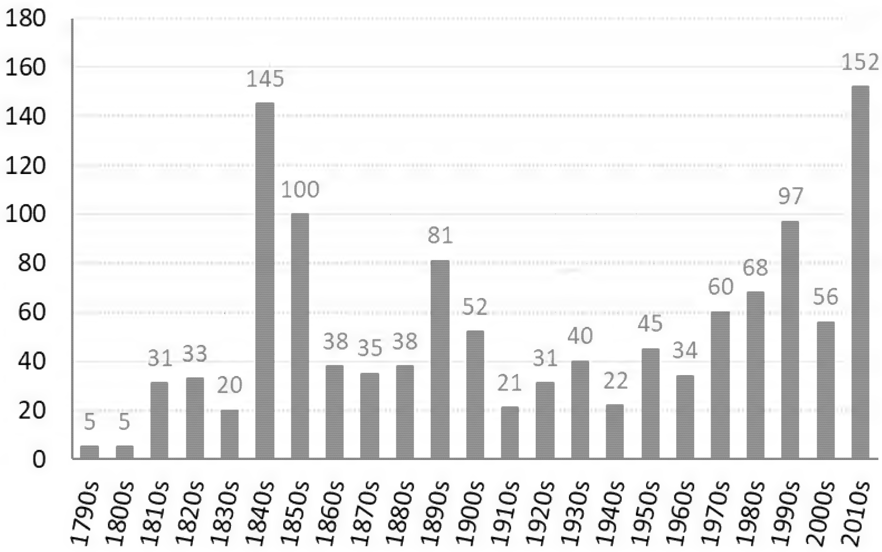

Figure 2. Species descriptions per decade of Western Australian macroalgae.

tropics virtually untouched and unknown. Recent expeditions mounted by the Western Australian Museum to examine the marine biodiversity of the north-west coast have enabled the collection of seagrass and macroalgal specimens throughout the tropics. Numerous publications have resulted, with much of the macroalgal information collated in two volumes in the 'Algae of Australia' series (Huisman 2015, 2018). These included 522 species (351 red algae, 110 green algae and 61 brown algae), of which 92 were new to science.

RECENT ADVANCES

Two methodological advances have had a significant impact on our understanding of marine plant taxonomy and biogeography, namely DNA sequence analysis and the use of 'big data'. DNA sequence analyses have facilitated both species identification through the establishment of 'barcodes', and phylogenetic assessments. 'Barcoding' can ensure accurate identification, the proviso being that the reference sequence used for comparison is indeed representative of the named species. One clear trend arising from molecular analyses is that in most cases there are more species than have previously been named. An extreme example was highlighted by the studies of the red algal genus *Portieria* by Payo *et al*. (2012) and Leliaert *et al*. (2018), who tested species boundaries based on mitochondrial, plastid and nuclear encoded loci, using a general mixed Yule-coalescent (GMYC) model-based approach and a Bayesian multilocus species delimitation method. They found that the then current morphology-based assumption that the genus includes a single, widely distributed species in the Indo-West Pacific (*Portieria hornemannii*), was not supported, and they recognized 21 species within the Philippines alone. Species distributions were found to be highly structured with most species restricted to island groups. Leliaert *et al.* (2018) subsequently broadened the Payo (2013) study to include specimens collected from additional localities in the Indo-Pacific, and reported a staggering 92 species-level lineages. Similar studies of other seemingly widespread species have also revealed previously unrecognized species diversity. The brown alga *Lobophora variegata*, for example, also regarded as morphologically variable, may encompass over 100 species (Vieira *et al*. 2014).

Molecular methods have also impacted our understanding of individual species. In south-western Australia lives a species of the otherwise almost wholly tropical green algal genus *Halimeda.* Originally described from South Africa as *Halimeda cuneata*, the species was recorded for south-west Australia by Womersley (1956, 1984) based on convincing morphological evidence. Cremen *et al.* (2016) undertook a detailed morphological and molecular study of '*Halimeda cuneata*', their DNA sequence analyses demonstrating that specimens identified by morphology as *H. cuneata* in fact formed several species-level lineages, including two from South Africa and one from south-west Australia. Thus the Australian taxon could no longer be identified as *H. cuneata*, and the name *Halimeda versatilis* J. Agardh, based on a specimen from Cape Riche, was restored from synonymy.

Conversely, molecular methods have also demonstrated the presence of seemingly introduced species in Western Australian seas. Recently, a species of the green alga *Codium* was collected from the Walpole/Nornalup estuary on the south coast. This alga was initially thought to be a new species (Huisman *et al.* 2011), but DNA sequence analyses indicated conspecificity with the South African species *Codium tenue* (Huisman *et al.* 2015). Remarkably, this species is rare in Western Australia where it is known only from muddy estuarine locations, a habitat mirrored precisely by the equally rare species in South Africa. How *Codium tenue* came to be established in southwest Australia can only be speculated on.

Molecular methods have thus led to the recognition of cryptic and pseudocryptic species: those that cannot be distinguished by morphology and those with diagnostic features only recognized following guidance by molecular analyses, respectively. This process has been described as 'molecular assisted alpha taxonomy' (Saunders 2005) and has been adopted in most recent studies. However, traditional taxonomy cannot be ignored as appropriate names have to be applied to barcode sequences. There is still a need for the field-biologist to be able to identify what species they are working on, recognizing in the case of some algae this may be an impossible task. Given the presence of cryptic species, it becomes imperative that barcode sequences are generated from type material or at the least putatively authentic material from the type locality. The commonly held belief that many species are widespread and encompass considerable morphological diversity can no longer be regarded as indisputable. Past species records based on morphology, particularly of seemingly widespread taxa, will need to be reassessed. In many cases this will not be achievable, particularly for the countless records based on formalin-preserved specimens, a preservation that renders them useless for DNA analysis. Even if methodologically feasible, it is unlikely that resources will be directed towards barcoding entire herbarium collections. Undoubtedly, DNA barcoding will ultimately result in taxonomic clarity, but the road to enlightenment might be long and arduous. Clearly, the first target should be establishing a barcode reference library based on sequences obtained from type material, or if unavailable then authentic specimens collected from the type locality, their identities verified by an experienced taxonomist.

The second major advance is the use 'big' data. All information pertaining to plant specimens (including the algae) housed in the Western Australian Herbarium (DBCA) is recorded in a database and made available through the Herbarium's portal 'FloraBase' and, combined with records from other Herbaria, additionally through the 'Australasian Virtual Herbarium' and the 'Atlas of Living Australia'. The ready availability of these records (which includes names, localities, dates etc.), potentially allows for assessment of range shifts and local extinctions, assuming the initial records are comprehensive enough to permit such assessments.

While the methodological advances described above will clearly enhance our taxonomic knowledge, and ultimately provide tools to enable rapid identification of specimens, their impact on biodiversity assessments

and marine conservation efforts must also be considered. Visual field surveys lacking vouchers, already unreliable due to the difficulty in identifying all but the common species (see Fig. 3 for example), will potentially underestimate the actual biodiversity by orders of magnitude. Conservation efforts must take into account the possibility of small-range endemics and not assume that marine species are resilient based on an assumed large geographical range.

RANGE SHIFTS

The availability of historical, geolocated specimen records, if adequate and used appropriately (Huisman & Millar 2013), can enable assessments of range shifts due to climate variation and other factors. The west coast, with its essentially north–south alignment and latitudinal (= temperature) gradient, provides an ideal setting for assessing the susceptibility of marine species to variations in sea temperature. Range shifts along the coast of Western Australia are not a recent phenomenon, with species undoubtedly impacted by historical variations in the strength of the southerly flowing warm Leeuwin Current. An interesting example was provided by Harvey, who in 1855 described the essentially tropical green alga *Penicillus nodulosus* (as *P. arbuscula*) as "abundant, on shallow sand covered reefs at Rottnest". This species has not been observed at Rottnest in recent times. The presence in south-western and southern Australia of tropical species (e.g. *Acrosymphyton taylorii* I.A. Abbott) or endemic species of otherwise tropical genera (e.g. *Gibsmithia womersleyi* Kraft), also suggests past periods or influxes of warmer water and the establishment and maintenance of these species in refugia.

A dramatic example of the impact of elevated sea temperatures was the recent decline of the temperate fucalean brown alga *Scytothalia dorycarpa* (Turner) Grev. from the Jurien Bay region, following an extreme warming event (Smale & Wernberg 2013; Wernberg *et al.* 2013), leading to a shift in community structure towards a depauperate state. Similarly, the recent loss of large tracts of habitat forming seagrass from Shark Bay released an estimated 2–9 million metric tonnes of carbon dioxide into the atmosphere within three years (Arias-Ortiz *et al.* 2018) and the seagrasses are showing little sign of recovery (Nowicki *et al.* 2017). It is of course hoped that such declines are isolated and temporary, but given future scenarios describing higher temperatures and more frequent extreme events this is unlikely.

Changing species names present a practical problem for non-taxonomic specialist users. Environmental managers are particularly at risk of not knowing how to access the changing information, as they are required to be across a substantial breadth of information and often need to make decisions quickly (Lynch *et al.* 2015). For example, *Cladophora montagneana* Kütz. was the main nuisance green macroalga in the eutrophic Peel Inlet and was so dominant that algae was removed by bulldozers from shorelines and the shallow waters in 1970s and 1980s. This species has recently undergone a name change based on molecular analyses (Boedeker *et al.* 2016) and is now known as *Willeella brachyclados* (Montagne) M.J. Wynne (Wynne 2016). In years to come, managers could wrongly assume there was a shift in algal species composition in the Peel–Harvey estuary. This example presents other potential difficulties. The type locality of *W. brachyclados* is Cuba, yet the samples used to represent this species in the molecular analyses of Boedeker *et al.* (2016) were collected from Western Australia and New Zealand. Given the very real possibility of cryptic species, basing a name change on results derived from specimens collected from different oceans and hemispheres could be misleading.

Similarly, historical Western Australian records of the seagrass *Heterozostera tasmanica* must now be interpreted

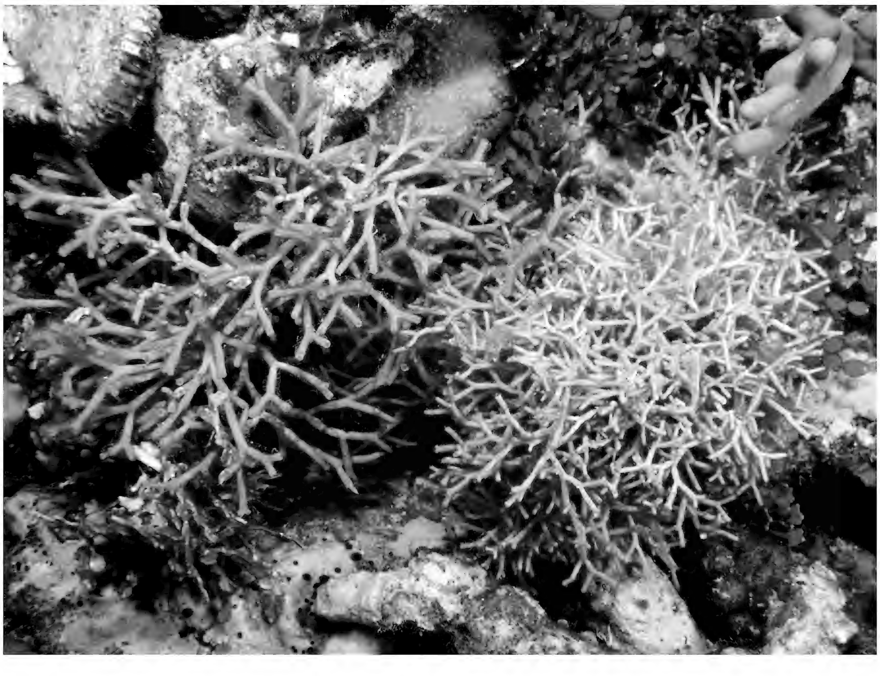

Figure 3. The similar looking red algae *Galaxaura pacifica* (left) and *Tricleocarpa fastigiata* (right) at Hibernia Reef, illustrating the difficulty in identifying species in situ.

as either *Heterozostera nigricaulis* or *H. polychlamys* as *H. tasmanica* is now not considered to occur in Western Australian waters. If relevant voucher specimens were not retained, it will be impossible to assess which of the two species the earlier records refer.

Worldwide, conservation policies and legislation also rely on species names to list for protection. For example, the Australian Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) contains a list of threatened species and ecological communities. Species listed are considered in categories of critically endangered, vulnerable, conservation dependent, extinct in the wild, and extinct, and includes as 'species' sub-species and distinct populations at the Minister's discretion for the purposes of the Act. For the marine flora, currently no species are considered conservation dependent or extinct in the wild, but the vast majority of species (certainly in the macroalgae) are data deficient and their true conservation status is unknown. Many species of algae are under-collected—their apparent rarity most likely due to historical disinterest or logistical difficulties—potentially leading to unsupportable assumptions regarding their status. It remains important for conservation to know whether something is locally endemic, or more widely distributed, and rapidly evolving taxonomies (with concomitant name changes) may not be reflected in legislation leading to either over-conservative, or inadequate conservation measures.

CONCLUSION

The marine flora of Western Australia is highly diverse, yet despite significant advances in molecular tools that can complement traditional taxonomy, the task of accurately assessing the diversity and biogeography remains problematic. The advances in barcoding molecular samples will lead us to very different and unexpected understandings as whole ecosystem assessments may be assessed using environmental DNA or "bar coding water samples". These challenges are not faced by WA alone—although the physical size of the marine environment (relative to the number of active research scientists) makes our challenge potentially greater.

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The origin of tiger snakes on Carnac Island

MITCH LADYMAN [1], EARLE SEUBERT [2] & DON BRADSHAW [3*]

[1] *School of Biological Science, Edith Cowan University, Joondalup, WA 6027, Australia*

[2] *Friends of Woodman Point Quarantine, 74 O'Kane Court, Munster, WA 6166, Australia (deceased)*

[3] *School of Biological Sciences, The University of Western Australia, Crawley, WA 6009, Australia*

* *Corresponding author:* ✉ *don.bradshaw@uwa.edu.au*

Abstract

Despite considerable research on the origin of the tiger snakes (*Notechis scutatus*) on the small island of Carnac off the coast of Perth in Western Australia, their source remains a mystery. Small morphological and ecological differences between the Carnac snakes and tiger snakes in other parts of Australia have been taken to suggest an unique lineage, but this is confounded by the possibility of colonisation of the island during the last marine transgression some 7000 years ago. Tiger snakes are also present on nearby Garden Island and elapid snakes are excellent swimmers. On the other hand, anecdotal reports suggest that the snakes were deliberately released on the island in 1930 by a snake handler. Information from the National Archives shows, with high probability, that this island population was established from a small number of snakes released in the early decades of the 20th century and that the scenario of isolation due to marine transgression does not apply. Now, interpretations of population-specific phenotypic and genotypic variations in the ecology, ecophysiology, demographics of the Carnac Island tiger snakes can be made with more confidence, based on the resolution that the population is less than 100 years old.

Keywords: phenotypic plasticity, adaptive evolution, island, evolution, ectotherm, reptile, snake, *Notechis scutatus*

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INTRODUCTION

The biology of island tiger snakes is well known and well documented. This large elapid occurs in high densities on islands along the southern coast of Australia and on the adjacent mainland in contrasting conditions (Shine 1987; Schwaner & Sarre 1990; Schwaner 1991; Bonnet *et al.* 2002). Moreover the populations show very low levels of genetic divergence at the molecular level (Scott *et al.* 2001). Within south-eastern Australia, where populations of island giants, island dwarfs, and mainland tiger snakes co-occur, the maximum genetic divergence is only 0.38% (Keogh *et al.* 2005). Structure plots currently being generated show a clear picture of relatedness between neighbouring populations with overall clinal variation from the eastern states to Western Australia (G Thomson pers. comm.).

This ecological scenario (isolated populations existing in close proximity to mainland conspecifics) presents novel opportunities to investigate adaptive evolution and exaptation (Gould & Vrba 1982), primarily because of the variable time since separation of the sub-populations. In many cases (southern Australia and Tasmania) populations have been separated for 5000–7000 years, and in all cases not more than 10 000 years (Keogh 1998). In each case, the closest relatives of the giant or dwarf populations on islands are mainland tiger snakes and the most proximate island and mainland populations are, in most cases, the most-closely related (Keogh *et al.* 2005).

Carnac Island, located less than 7.5 km off the coast of Western Australia and 10 km from the port city of Fremantle (Fig. 1), supports a population of Western Tiger Snakes. Keogh *et al.* (2005) and G Thomson (pers comm.) suggests these snakes are most closely related to conspecifics from local lakes throughout the inter-dune swales of the mainland Swan Coastal Plain, less than 15 km to the east of Carnac Island. These snakes have been the subject of considerable scientific attention over the last decade and a half (Bonnet *et al.* 2002; Ladyman & Bradshaw 2003; Aubret *et al.* 2004a,b, 2006; Bonnet *et al.* 2005; Ladyman *et al.* 2006; Aubret & Shine 2007, 2009, 2010). Each of these studies has shown clear and consistent patterns of dimorphism in behaviour, ecology, breeding biology, growth trajectories and physiology, driven by differences in the microhabitats present on the mainland and Carnac Island rather than by genetic divergence and natural selection. Nevertheless, some traits that differed between individuals within the populations were attributed to genetic divergence: these were traits measured as different at birth. Scale counts and relative jaw length were two such traits (Aubret *et al.* 2004a).

More recently, studies on the Carnac Island snakes considered the relative contribution of the two major drivers for polymorphism: phenotypic plasticity and adaptive evolution. Using this ideal ecological model as a basis, Aubret & Shine (2009) concluded that phenotypic plasticity was the primary driver when the snakes first

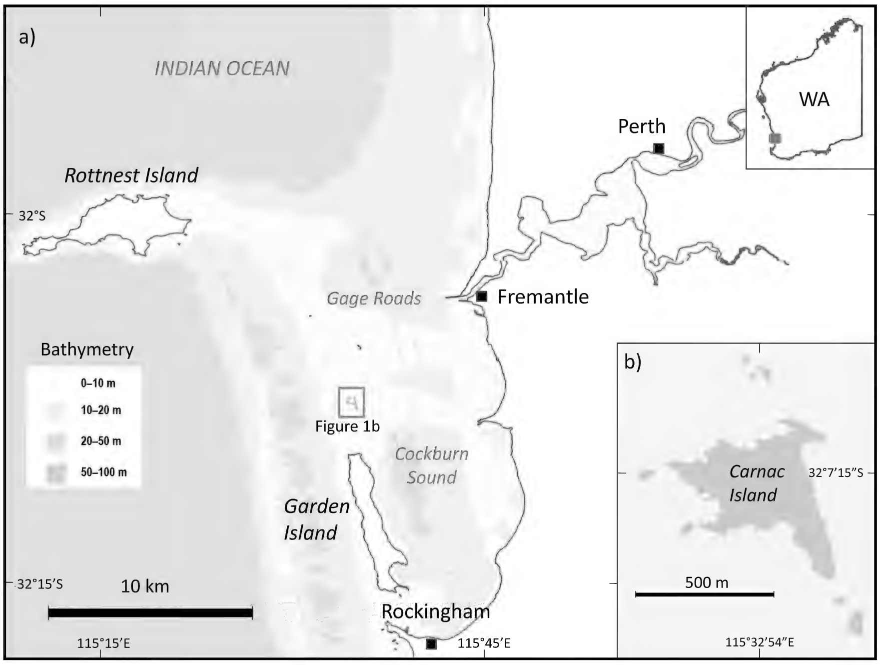

Figure 1. Location of Carnac Island relative to Rottnest Island, Garden Island and Fremantle, Western Australia (bathymetric image from GeoView.WA, Department of Mines, Industry Regulations and Safety using data from the Royal Australian Navy and the Department of Transport Marine Division).

colonise these novel island environments but, over time, changes in the genome are canalised to become fixed at birth. The benefits of these canalised traits lead to greater fitness over the life of an individual that possesses phenotypic traits of value at birth. Alternatively, individuals suffered an opportunity cost if these same traits were required to develop throughout the growth phase, regardless of their capacity to do so (Aubret & Shine 2009).

For the majority of studies referenced herein, the time since separation of the populations was not a dependent variable from which conclusions were drawn about adaptive evolution. In most cases conclusions simply described the differences between mainland and Carnac Island populations relative to the differences in their respective habitats and in the absence of genetic divergence and these differences were attributed to the exaptive potential of the reptilian bauplan (Bradshaw 1986).

But for the studies that seek to determine the role of phenotypic plasticity in novel environments versus genetic divergence in older populations, there is a fundamental requirement to know the age of the population, or the time since separation. This is because, although the adaptive advantages of phenotypic plasticity versus genetic assimilation are obvious, the relative rates of change of these drivers are more difficult to determine.

Conclusions reached with respect to the Carnac Island snake population have been based on the premise that the population is less than 100 years old and test individuals were the descendant progeny of a small founder population of some 40 snakes released on the island by a travelling showman called Lindsay Vagne (aka Rocky Vane) in 1930. However, for these conclusions to be valid requires a level of certainty that this was the only origin of the snakes and that the population did not arise as an isolated relic about 5000–10 000 years ago as a result of marine transgression (Playford 1983). We believe that the required level of certainty about the origin of the Carnac Island population has eluded previous scholars.

FEASABILITY OF A NATURALLY-OCCURRING POPULATION ON THE ISLAND, 1829–1930

Given that there is a naturally-occurring population of tiger snakes on adjacent Garden Island, and that tiger snakes are excellent swimmers known on near-shore islands, it is perfectly reasonable to expect that they would have been present on Carnac before 1930. However, at 19 ha, Carnac Island is far smaller than any other island along the west coast of Australia that supports a stable population of large elapid snakes. Along the entire central and south west coast no islands smaller than 1000 ha are known to support a naturally-occurring population of a large elapid snake. Garden Island, Rottnest Island and Barrow Island all support elapids and each is greater than 1500 ha. Early records by naturalists also do not document the presence of tiger snakes on Carnac Island.

THE LACK OF EVIDENCE OF SNAKES ON THE ISLAND 1829–1930

Our research has revealed the existence of early newspaper and other articles that suggest snakes did not occur naturally on the island. They also provide clues as to why a snake showman would choose to release snakes on the island in the first place.

The first article of note was an anonomyous letter to the Editor the West Australian Newspaper describing Carnac Island as a delightful and convenient resort only an hour or two's sail from 'the town' (Fremantle; Anon. 1878). The article was written as an expression of the

author's distress that access to the island by the general public was, at that time, being denied by the lessees who had stocked the island with rabbits for the purpose of hunting. The author's grievance about limited access to the island was that there was no alternative destination. Garden Island has too many snakes and Rottnest Island has too many other issues. The article unequivocally states that there are no snakes on Carnac Island. [1]

Carnac Island was also used as a quarantine station for many years prior to the turn of 20th Century. During this time up to 275 people, all who had showed signs of illness during passage from Europe to Australia, were detained on the island (Anon. 1897). A search of the National Archives revealed articles describing the tent village in which the detainees were housed, the means of transportation of food and water from Woodman Point to Carnac Island and the many trials and tribulations endured, but none of these articles mentions the presence of snakes. Given the origin of the detainees (predominantly from England) and their prior lack of exposure to venomous snakes, one would expect the presence of a large and highly venomous elapid to feature prominently in any communications about life on Carnac Island. The majority of these articles is dated between 1850 and 1920. It is only anecdotal evidence in Abbott (1978) that tiger snakes are first mentioned as present on the island by the early 1960s. A search of the reptile database of the Western Australian Museum found that the earliest records of tiger snakes from Carnac Island are in 1982 (Accession Nos R4975, R12818 and R12827), collected by Dr Dom Serventy, Eric Car and Harry Butler respectively, with a large collection by Dr Terry Schwaner in 1985.

EVIDENCE FOR THE RELEASE OF SNAKES BY ROCKY VANE

The evidence we present to support a 'recent release' hypothesis is subjective, as it is based on our interpretation of the content of letters and articles by early pioneers about life on an island with the mention of the lack of any snakes made only once (Anon. 1878), but notable in its absence on all other occasions. To further validate our conclusions requires an explanation as to why a snake showman would go to the trouble of releasing some 40 adult tiger snakes on Carnac Island that were clearly, based on structure plots, collected locally.

Originally from Melbourne, Victoria, Rocky would have been very familiar with snakes on offshore islands, with many populations naturally found off the Victorian Coast. Upon moving to Western Australia, Rocky lived in Fremantle and most certainly would have known of Carnac Island. Carnac Island was known to be devoid of fresh water and, during the years that it was used as a quarantine station, water was carted to the island in wooden vats. However, a well constructed in around 1903 yielded brackish water clean enough for washing and other purposes, though not fit for human consumption. Considerable effort was invested in the search for fresh water on the island with an article in the Western Mail, dated 20 March 1914, identifying the presence of two wells and a rain water tank (Anon. 1914).

We collected many articles documenting the almost constant troubles in which Rocky Vane found himself with the local law enforcement both in Western Australia and in the eastern states and the financial difficulties he faced as a travelling showman in another state. For instance, Rocky's first wife died of snake bite in 1928 and his new partner Harry Melrose was also bitten and died in 1929 (Bonnet & Pearson 2007). Rocky also faced court for using snakes to intimidate his new wife in 1931. In addition, Rocky's wealth and security were dependent entirely upon the success of his snake shows at carnivals such as White City/Coo-ee City and Uglieland, which were under threat of closure by the local law enforcement in the late 1920s in Perth and the early 1930s in Fremantle. Whereas the former carnivals closed in 1929, Uglieland continued operating in Fremantle until 1936.

If Rocky Vane was ordered by the courts to release his collection, as suggested in a newspaper report (Anon. 1931), he could easily have replenished his collection in a matter of days. This could have been done by collecting from local lakes around Perth, given the prevalence of tiger snakes on the Swan Coastal Plain (pers. obs).

Previously, evidence that the snakes were released on Carnac Island in 1930 was based on only anecdotal references that are difficult, if not impossible, to verify. Aubret *et al.* (2004b) cite a personal communication from Dr Terry Schwanner, who had published extensively on island tiger snakes in the eastern states of Australia. Though there is a strong possibility that this story is true, there is a lack of clear evidence as to whether or not snakes existed on the island prior to their supposed release in 1930.

An exhaustive search of the newspaper archives in the National Archives failed to reveal any evidence to validate or verify the story concerning the release of the snakes by Rocky Vane. The most sound evidence—still ambiguous at best—was a short newspaper article called 'Snakes in Bed' (Anon. 1931) in which Rocky was reported to have told the court that he had "gotten rid of his snakes" during a court session where he was facing reprimand for harassment of his (then) wife.

Following an order of the Court to release his snakes, and having only been in Western Australia for a very short time, it is unlikely that Rocky Vane would have known anyone with whom he may have agisted his collection. Therefore Carnac Island may have provided an ideal potential temporary repository. Although covering just 19 ha, the island was large enough to support the snakes, small enough for him to retrieve them and easy enough to access by boat from Fremantle.

However, he was noted by a local newspaper to be back in possession of several snakes, which were housed in his tattoo shop in James Street in 1933 (Anon. 1933) and he was bitten again during a display in Rockingham in 1934 (Anon. 1934). These articles provide clear evidence that, though he was forced to release his snakes, he never intened to be without them for very long. A short journey

[1] Twenty eight of the first settlers to WA were initially put ashore on Carnac Island in June 1829 for some days. They complained about the lack of cutlery (James 2007), but no mention was made of snakes.

from Fremantle, Carnac Island would have presented a simple solution to this misfit's agistment problem.

CONCLUSION

We offer better than anecdotal evidence concerning the origin of the Carnac Island tiger snakes and give some certainty as to the question of the age of the population and the time since its isolation from the mainland. We are confident that there was no self-sustaining population of tiger snakes on the island prior to Rocky Vane's release in 1930. If accepted, this means that any differences between island and mainland populations must have developed in the intervening 90 years, rather than the many thousands of years for which Carnac has been an island. Whereas our interpretations are subjective, this suite of archival evidence goes a long way to validating many of the conclusions of Aubret & Shine (2009) thereby supporting the notion that phenotypic plasticity is most valuable and prevalent in novel environments recently colonised by snakes.

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Are Karda (*Varanus rosenbergii)* more abundant around traditional Noongar lizard traps?

LARISSE GUISLAIN [1,2]*, LYNETTE KNAPP [2], ALISON LULLFITZ [2] & PETER SPELDEWINDE [2]

[1] *Bristol Veterinary School, University of Bristol, United Kingdom*

[2] *Centre of Excellence in Natural Resource Management, University of Western Australia*

**Corresponding author: ✉ larissesophie@me.com*

Abstract

Construction of lizard traps on granite outcrops is a traditional hunting method used by the Menang Noongar people of southern coastal southwest Australia for *Varanus rosenbergii* (also called Karda by the Noongar, or Rosenberg's Monitor by Europeans); an important protein source in pre-colonial diets. This method may have been employed to increase the abundance of this species or to aid access to this resource. To explore this question we combined Noongar traditional knowledge and western scientific techniques to investigate the abundance of lizard traps in relation to intensity of pre-colonial Noongar use and Karda abundance.. We found lizard traps were evenly distributed on granite outcrops across our study area regardless of likely past intensity of use by Noongar people. Using camera trap data and occupancy modelling we also found that Karda abundance was uniform across our study area and did not appear to be influenced by the presence of traps, indicating that their construction may have been to facilitate hunting rather than to increase their number.

KEYWORDS: Noongar, OCBIL, YODFEL, Traditional ecological knowledge, Varanus lizard

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INTRODUCTION

For tens of millennia, interdependent relationships have existed between humans and other organisms, including the human modification of habitats to aid access to food and other resources (Smith 2011; Tobler *et al*. 2017; Bliege Bird *et al*. 2013; Groesbeck *et al*. 2014; Lullfitz 2019). Habitat modification methods employed by traditional societies include construction of aquatic, marine, or terrestrial structures (e.g. fish weirs) to enhance abundance or to assist capture of resource organisms (Smith 2011). For example, 'clam gardens' constructed by First Nations people of Northwest Coastal America have been found to maximize clam productivity (Groesbeck *et al*. 2014), whereas pit traps constructed by people in pre-colonial southwest Australia were used to aid kangaroo hunting (Nind 1831) but would not have enhanced abundance.

Southwestern Australia is dominated by old, climatically buffered, infertile landscapes (OCBILs) within a mosaic of younger, often disturbed, fertile landscapes (YODFELs; e.g. coastal dunes and wetlands; Hopper 2009; Hopper *et al*. 2016). Southwest Australian examples of OCBILs include granite outcrops and quartzite uplands, which exhibit high levels of endemism and specialized organisms compared to YODFELs (Hopper 2009; Hopper *et al*. 2016). Rocky outcrops support high levels of biological diversity (Goldsbrough *et al*. 2002; Porembski 2007). Loose surface rocks are important reptile microhabitats (Croak *et al*. 2010). In Australia, an estimated 60 reptile species predominantly live on rocky outcrops of which at least 20 are found principally on granites (Wilson & Swan 2013).

Southwestern Australia has been home to fourteen groups of the Noongar nation for at least 48 000 years (Turney *et al*. 2001). Our study area falls within Menang Noongar country (Fig. 1). Archaeological and ethnographic studies indicate that Menang occupation patterns heavily utilized coastal dunes, estuarine fringes and wetland areas (all YODFELs), whereas use of granite outcrops (OCBILs) was prevalent, but less frequent and often restricted (Lullfitz 2019; Goode *et al* 2005; Applied Archaeology Australia 2012).

Varanus rosenbergii (in Noongar, Karda) plays a key role in Menang culture, featuring in dreaming stories, and its eggs and meat provided a valued protein source (Guilfoyle *et al*. 2013; Tilbrook 1983; Bindon 1997). As a Meananger elder, LK attests that eggs would be gathered from termite mounds, whereas Karda were hunted by driving them up trees or by using lizard traps.

A lizard trap consists of a rock slab propped up by smaller rocks, and does not 'trap' the animal per se (Fig. 2). These purpose-built structures mimic the natural habitat for reptiles on granite outcrops (Bindon 1997). Reptile species targeted by the Menang Knapp family include Karda, blue-tongued skink (*Tiliqua rugosa*) and carpet python (*Morelia spilota*). Previous studies suggest the role of lizard traps as habitat-enhancement or resource enrichment for reptiles (Bindon 1997; Guilfoyle *et al*. 2013; Mitchell 2016). However, there is currently a lack of quantitative studies to support this. LK describes

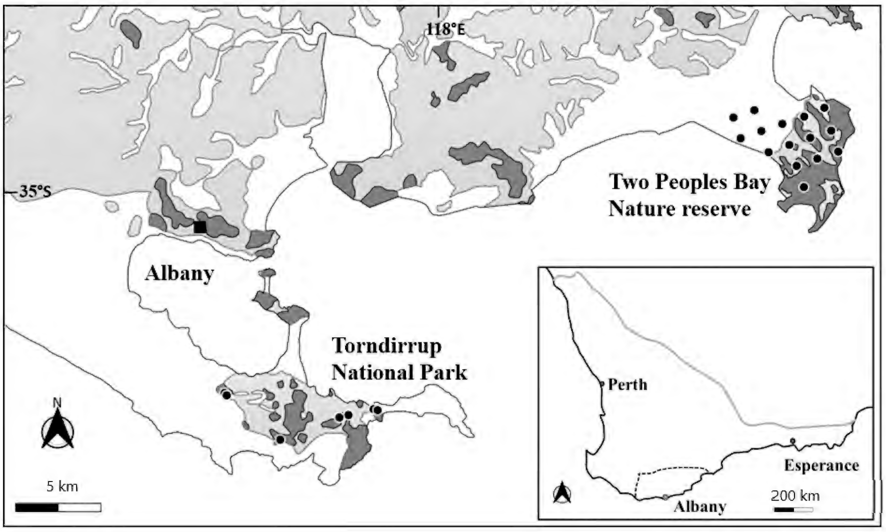

Figure 1. Study sites at Torndirrup National Park and Two Peoples Bay Nature Reserve, near the city of Albany, and soil landscape classifications. OCBILs (dark grey), YODFELs light grey), and areas which do not fall into the strict classification of OCBIL or YODFEL (medium grey). The inset map shows the region inhabited by the Noongar people in a solid grey line, Menang country in dashed line, and towns of importance. Map created using using landscape soil subsystem data from the Department of Agriculture and Food Western Australia (Purdie *et al*. 2004).

Figure 2. Examples of lizard traps: a) and b) at Two Peoples Bay Nature Reserve; c) and d) at Torndirrup National Park.

that whereas all granite outcrops were used for hunting Karda using lizard traps, outcrops closer to camps would likely contain more. LK also notes that Karda are difficult to catch in summer due to high surface temperatures, and that use of lizard traps for hunting is primarily confined to the cooler months.

We hypothesized that granite outcrops close to YODFELs (areas more heavily utilised by Menang people), including dunes, and estuarine and wetland fringes, would have a higher abundance of lizard traps than those at greater distance. Secondly, if lizard traps act as habitat enhancement, then more Karda would be

detected where lizard traps were more abundant. This study aimed to investigate these hypotheses, especially whether habitat modification through lizard trap construction increases Karda abundance.

METHODS

This study was conducted in Menang country in the Two People's Bay Nature Reserve (TPBNR) and Torndirrup National Park (TNP) close to the City of Albany (Fig. 1). Landforms of the study area were categorized as YODFEL, OCBIL or neither in accordance with Lullfitz. (2019) using landscape-soil subsystem data from the Department of Agriculture and Food Western Australia (Purdie *et al*. 2004).

Lizard traps were counted on granite outcrops at 22 locations across TPBNR (15 sites) and TNP (seven sites). The TPBNR sites were pre-determined locations of the camera traps (see below) whereas TNP sites were chosen for ease of access and distribution across the landscape. No camera trap data was available at TNP. For each site, the total survey area was recorded and then the count standardized to number of traps per metre of granite surveyed. Surveys were limited to a maximum of one hectare. Surface granite features were identified as lizard traps where a prop rock was clearly present but were not included where human construction was determined to be ambiguous (e.g. natural exfoliation).

To estimate Karda utilization of habitat, camera trap data for TPBNR was acquired from the West Australian Department of Biodiversity, Conservation and Attractions for routine feral cat monitoring. Data was collected using Reconyx Hyperfire HC600 (Reconyx, Wisconsin; USA) passive infrared camera traps set 1 km apart deploying a total of 15 cameras. The data acquired for this study covered November 1, 2014 to February 28, 2015.

A 50 m transect was surveyed in each cardinal direction from each camera trap. Along each transect, average shrub height, total bare ground, granite and other rock coverage were recorded. All termite mounds and ant hills within one metre of each transect were also recorded.

A spatial occupancy model was analysed to determine the probability of Karda at various OCBIL and YODFEL sites at TPBNR. The detection of an individual on a camera confirmed that the species was present at the site. However, non-detection does not necessarily mean the species was absent (MacKenzie *et al*. 2017). Occupancy values were generated by assuming probability of detection remained constant whereas an adjacency matrix accounted for the possibility of individuals ranging across more than one camera. The spatial model of Comer *et al*. (2018) was run on WinBUGS (v14; Lunn *et al*. 2000) with a burn in of 5000 iterations and sampled for 2000 iterations.

A Pearson's correlation test was used to analyse for correlation between lizard trap abundance and distance to nearest YODFEL, and Karda occupancy values and distance to nearest YODFEL. A step-wise linear regression was utilised to identify deterministic factors for Karda occupancy. Factors in this analysis included average shrub height, number of ant hills, total bare ground, granite and other rock coverage, distance to nearest OCBIL and YODFEL. All statistical analyses were carried out using R version 3.5.1 (R Core Team 2016).

RESULTS

Of the total 22 sites in our study area, 12 included granite outcrops. Across these, the density of lizard traps was 0.01(±0.013) per m^2 of granite surveyed. At two sites none were recorded. We found no correlation between lizard traps and distance to nearest YODFEL (R^2= 0.008, p= 0.64; Fig. 3a).

Occupancy values showed Karda had a high detection probability (0.857±0.002) across all 15 sites at TPBNR. Regression results indicated distance to YODFEL explained some variation in occupancy (R^2 = 0.48, p <0.01; Fig. 3b), with a slightly higher occupancy at lesser

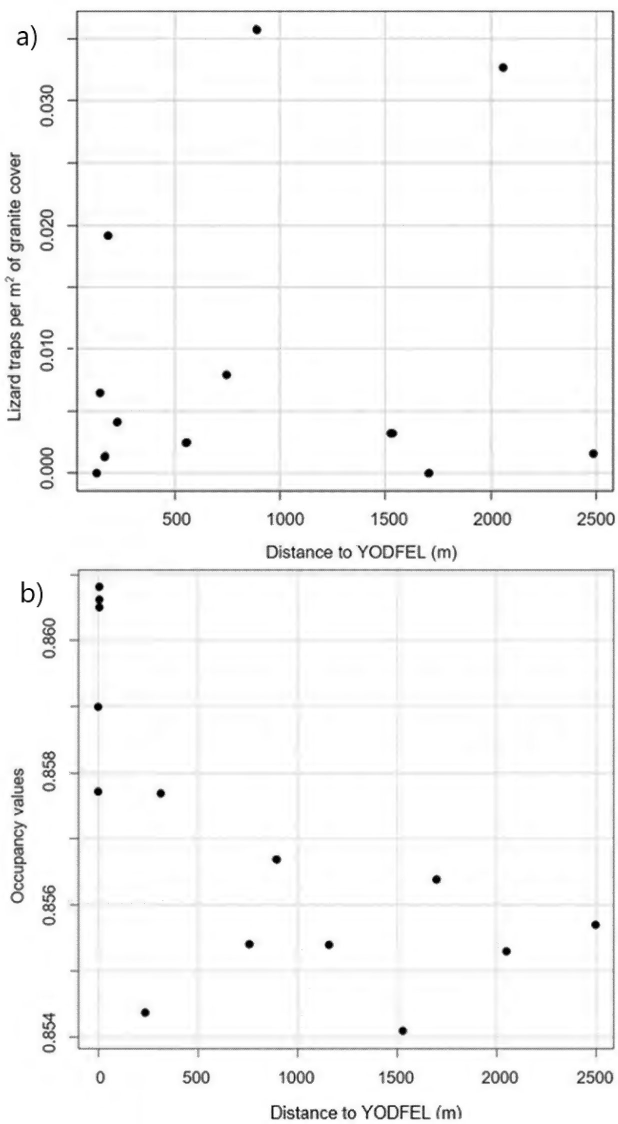

Figure 3. Scatterplots: a) count of lizard traps per square metre of granite surveyed and the direct distance to nearest YODFEL (m) for each site; and b) regression analysis between the occupancy values of karda at each site and distance to YODFEL (m).

distances. However, the overall range of occupancy values was very small (0.854 – 0.861). Karda detection rates did not differ between non-granite sites, granite sites with lizard traps, and granite sites with no lizard traps (Chi-squared = 4.768, p = 0.09, df = 2).

Occupancy values for Karda were driven by distance to nearest OCBIL, granite cover, and number of ant hills (probability of occupancy = 0.09487 + 1.872 x 10^{-6} x OCBIL - 17.879 x 10^{-6} x granite cover - 623.978 x 10^{-6} ant hill). However, occupancy range was minimal.

DISCUSSION

Our findings do not support the hypothesis that abundance of lizard traps on granites close to YODFELs heavily used by Noongar people is higher than those farther away, or that Karda are more numerous at sites where lizard traps are more abundant. These results indicate that Noongar habitat modification through lizard trap construction may not increase Karda abundance.

Although OCBILs were occupied less than YODFELs by Menang people, reptiles may have been more important than other protein sources during periods of OCBIL occupation than at other times. Given that macropod hunting (and mosaic burning for hunting) was carried out more often in YODFELs than in OBCILs (Lullfitz 2019), this could be a plausible reason for the lack of variation in lizard trap abundance with distance to YODFELs. This question warrants further investigation through collaborative research to understand Noongar pre-colonial diets, specifically in relation to ceremonial events.

Lizard traps are by nature stable once constructed. To this end, we assumed they would not be readily dismantled by people, and that constructed lizard traps would have accumulated over time. This may explain their homogenous frequency across granites surrounded by OCBILs and YODFELs. Alternatively, there may have been post-colonial removal of lizard traps from granites for ornamental or landscaping use (Shine *et al*. 1998; Goode *et al*. 2005) given the proximity of the study area to a major urban centre.

Uniform Karda occupancy across all TPBNR sites suggests that lizard trap abundance does not result in increased Karda detectability. Even though Karda occupancy was slightly higher at sites closer to YODFELs, overall variation in occupancy rates was so small (<1% difference between maximum and minimum values) that this was unlikely to have ecological significance.

Although Karda were largely hunted by Menang people in the cooler months, our camera trap data was recorded during summer (November to February). Given that Menang use of lizard traps to hunt Karda in winter is based on observations of differential Karda behaviour between seasons, this may have influenced our findings. We also note that our study area and data set are small, and that a larger study taking in all seasons is warranted to clarify a possible relationship between lizard trap and Karda abundance.

Whereas our study indicates that lizard traps may not be vital habitat for Karda, this does not discount their heritage value or possible importance for other reptile species. In addition, our finding of uniformity in lizard trap abundance irrespective of past Menang land use, indicates that they may be an animal harvesting technology tailored for human survival within old landscapes. Further cross-cultural research will enhance a shared understanding of country and the long-held land practices of the First Nations people of southwestern Australia.

ACKNOWLEDGEMENTS

We are immensely grateful to the Menang people for allowing us to understand and appreciate their families' cultural practices and importance of country, and furthermore, to conduct this research. We thank the Department of Biodiversity, Conservation and Attractions and Sarah Comer for camera trap data, and Professor Stephen Hopper and two anonymous reviewers for providing feedback on the manuscript.

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Joseph John Edmund Glover

BSc (Hons, UWA), PhD (UC, Berkeley), Honorary Member RSWA

14th July 1924 – 11th February 2020

John Glover passed away in Perth on 11 February 2020 in his 96th year. He had been President of the Royal Society of Western Australia in 1961–62 and Honorary Editor of the journal of the Society from 1958 to 1963.

Joseph John Edmund Glover, always known as John, was born at Mt Barker, about 50 km north of Albany, Western Australia. His father Cecil had emigrated in 1910 from Britain and in 1918, after serving in the Australian infantry during WWI, acquired a farm near Mt Barker of about 500 acres, largely jarrah forest requiring clearing, under the Returned Servicemen Settlement Scheme. His mother Rhoda was a schoolteacher and author of *Plantagenet Rich and Beautiful: A History of the Shire of Plantagenet Western Australia* and another book for schools—John benefited from her expertise during his primary education under the State Correspondence Scheme, as the family lived too far from the town for him to attend school there.

John and his younger brother Eric grew up as country boys and, when John won a scholarship to Perth Modern School and boarded in Perth, he found that he was lacking social skills by comparison with town-raised boys. He went on to the University of Western Australia to study geology, boarding in St Georges College, but joined the RAAF in 1943, training in Canada as a wireless-operator air-gunner to serve in bombers. However, he was discharged in 1945 as a Flight Sergeant, shortly after Hiroshima, without having seen active service. He returned to UWA, again boarding at St Georges College where he was President of the Junior Common Room in his final year, and gained a BSc with first-class Honours in geology as well as collecting two prizes (jointly with Basil Balme) for his thesis in 1947.

His first employment as a geologist was in 1949 with the Bureau of Mineral Resources doing fieldwork mainly in Queensland and the Northern Territory. In 1950 he was awarded a Fulbright Scholarship and a Smith-Mundt Grant allowing him to undertake a PhD at the University of California, Berkeley, in the USA. His thesis on coastal sediment movement at Santa Barbara was supported by the US Navy. In 1953 he returned to his employers, but later in the year joined Associated Australian Oilfields as a Project Leader for field parties in the Bowen Basin, Queensland, rising to Senior Geologist by the time he left in 1955.

His return to Perth in 1955 saw him at UWA as a lecturer and supervisor of Honours and PhD projects in geology. He was Head of Department from 1985 to 1988 and in 1985–86 presided over the Australian Council of Chairmen of Earth Science Departments. One of his significant contributions to the Department during this time was to raise funds and organise a complete refurbishment of the Department's geology museum, together with Professor Harris, as part of the celebration of UWA's 75 years in 1988. The E de C Clarke Geology Museum, which was opened in 1989 by the Deputy Premier of WA, is still being enjoyed by students and the public.

John in ~1997

John was a Foundation Member of the Geological Society of Australia. He was editor of their journal from 1970 to 1973, and Chairman of the Western Australian Division of the Society in 1968–1969. John was also an active member of the Gemmological Association of Australia and was on their WA Branch (now Division) council in the 1960s and 70s, including as Vice President and President—in 2006 he accepted the invitation to be patron of the WA Division, following Prof Rex Prider in the role. As well as his Geological Society of Australia and RSWA memberships, he was a Fellow of the Geological Society of London, a Fellow of the Gemmological Association of Australia and a Member of the New York Academy of Sciences. John also had *Cleiothyridina gloveri,* a spiriferid brachiopod, named after him by George Thomas in 1971.

In his research on sedimentary petrology, John collaborated with archaeologists, geographers and historians. This was unusual during the 1960s and 1970s, at least in Western Australia. John created links across the

at Bowen Basin field camp in 1953

divisions that then separated Geology, Geography and Archaeology—a collaboration spanning 1971–1993 that produced many papers on the provenance of Aboriginal artefacts during the last sea-level lowstand—at a time when interdisciplinary work of this kind was only just becoming fashionable. As was the case in those days, he was lead author on many of the resulting research papers in over 22 different refereed journals, including several in *Nature*. He also edited volumes arising from many important research symposia held at UWA in which he also made significant contributions to the minerals industry.

On retirement in 1990 John was appointed Senior Honorary Research Fellow and until 2014 worked almost daily in his room near the entrance of the Geology Building, assisting with postgraduate teaching, undertaking original research, writing books and editing. He produced a small textbook and ran intensive courses on scientific writing for Honours students both at UWA and elsewhere, including the staff of the Volcanological Observatory in Rabaul, PNG where he experienced volcanic eruptions at first hand. He also contributed 140 articles for the *West Australian Geologist*, the newsletter of the Geological Society of Western Australia (WA Division) and, with the help of Jenny Bevan, published a compilation of selected topics that had been covered in these articles into a volume commissioned by the GSA (WA Division) for their 50th Anniversary: *Geological Journeys: from Artefacts to Zircon.*

During retirement, John decided to produce a comprehensive study tracing the careers and contributions of practically all the geologists, as well as notable prospectors and laboratory scientists, operating in Western Australia during the first century of European settlement. *The Forgotten Explorers: pioneer geologists of Western Australia 1826–1926*, was co-authored with Jenny Bevan and released by Hesperian Press in 2010. This well-researched book, launched with the help of Woodside, begins with historical and geological background information leading to the period and tells the stories of around ninety or so characters involved in geological discoveries over the period.

John Glover's contribution to geology at the University of Western Australia, spanning 75 years, from his entering as a student in 1939 and finally retiring as a Senior Honorary Research Fellow in 2014, was remarkable. He was a wise and gentle mentor to many staff. He also maintained a close association with St Georges College where he had been Resident Tutor during the 1970s. In 2010 he endowed a scholarship for students at the college in honour of his parents. Unsurprisingly, in 2004, he was awarded the UWA Chancellor's Medal for his service to the University throughout the years. The Geology Department also honoured him in 2011, naming the John Glover Meeting Room in the Geology Building after him.

In his later years, a road accident outside the university put John in hospital for some time and eventually, in 2014, he entered a local nursing home where he was well cared for and comfortable. Although suffering progressively failing health, he remained lucid and maintained his sense of humour, and enjoyed regular visits by old colleagues up to the weeks before his death from pneumonia. He is survived by his brother Eric and two nieces: Leanne and Janine.

Jenny Bevan

Former Senior Curator, E de C Clarke Earth Science Museum and Honorary Research Fellow,
The University of Western Australia

David Haig

Honorary Senior Research Fellow
Oceans Graduate School
The University of Western Australia

This obituary is based mainly on autobiographical notes written by John in 2012, and includes material also published in an obituary in *The Australian Geologist*.

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The quest for Alfred Russel Wallace's house on Ternate, Maluku Islands, Indonesia

PAUL WHINCUP [1]

[1] *Independent Hydrogeologist, Jakarta, Indonesia*

✉ *paul.whincup@yahoo.com*

ABSTRACT

Wallace penned his famous essay on the theory of evolution through natural selection while based in Ternate and sent it to Charles Darwin in March 1858 from the house he rented there. Although two houses have at various times been designated by the City of Ternate as the official site of the Wallace House, the first, a traditional house, meets none of the criteria in the descriptions given by Wallace in his book *The Malay Archipelago* including the presence of a deep well. The second site, where the original house had been demolished long ago, fails in one key aspect—the presence of a fort just below it. Even if Wallace's House no longer exists, it is likely that the deep well he described, or remnants of it, would remain thereby allowing the site to be identified with some precision. A hydrogeological census in the general area described by Wallace found several old, deep wells and showed that one site closely matched all of the criteria he mentioned. This is named the Oranje Site and has been formally adopted by the City as the true location of the Wallace House. The City plans to purchase the site and build a replica of the house for use as a museum.

Keywords: Alfred Russel Wallace, Ternate house, old deep wells, Fort Oranje

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INTRODUCTION

During the second half of his sojourn in the Malay Archipelago, from January 1858, Wallace rented a house for three years in Ternate, a small volcanic island in North Maluku, about 2400 km east-northeast of Jakarta (Fig. 1). It was from this house that he penned his famous 'Ternate Letter' to Charles Darwin with an essay outlining his ideas on 'natural means of selection' (Wallace 1858). It was also here in 1859 (Wallace 1860) that he postulated the divide between Southeastern Asian fauna on the west and Australian fauna on the east, later named the 'Wallace Line' (Fig. 1) by Huxley (1868). In his book, *The Malay Archipelago*, Wallace (1869) provides several clues as to the location of this house, referring to features such as the market, the native quarter and the fort (Fig. 2). The site of this house has raised considerable interest over the years, with the City of Ternate having variously designated two locations as the official site. The first was the Sultan's House, occupied by family members of the Sultan of Ternate. The second, termed the Santiong House, was recognised by the local authorities in 2008, on the 150th anniversary of the despatch of the Ternate Letter, and the street on which it is situated was renamed 'Jalan Alfred Wallace'. In 2010 the name was changed to 'Jalan Juma Puasa' but the adjacent alley, 'Lorong A. Wallace', continues to have wall murals commemorating Wallace. Santiong meets most, but not all, of the points in Wallace's descriptions. It was argued that the true site could probably be identified with some accuracy by the presence of the old deep well. A hydrogeological survey of the area was singularly successful in identifying several deep wells, one of which is on a site closely matching all of Wallace's descriptions. The land on which it is located is named the Oranje Site. Given continuing advocacy for the Santiong House and some lingering support for the Sultan's House, it was not until September 2019 that the local authorities finally endorsed the Oranje Site as the true position of Wallace's House.

WALLACE'S CLUES FOR THE HOUSE'S LOCATION

Wallace, in *The Malay Archipelago* (1869, p. 232–234) gives the following clues (in italics), as to the location of his house on Ternate:

- *The house is surrounded by a wilderness of fruit trees. The lower part of the mountain, behind the town of Ternate is almost entirely covered with a forest of fruit trees, and during the season hundreds of men and women, boys and girls, go up every day to bring down the ripe fruit.* This description applies to what is now the suburb of Santiong, which hosts both the Santiong and Oranje Sites.
- *A deep well supplied me with pure cold water*. In all the deep wells the groundwater is 28°C, clear and uncontaminated—not cold, but certainly refreshing in Ternate's tropical environment. The electrical conductivity of the water is 300 µS/cm (drinking water standard is up to 800 µS/cm).
- *Five minutes' walk down the road brought me to the market and the beach*. The market is clearly marked on the Master Plan of Ternate (Reimer c. 1750) and the Map of Ternate (in De Clercq 1890). It is a 595 m walk from the Oranje Site, a shorter walk from

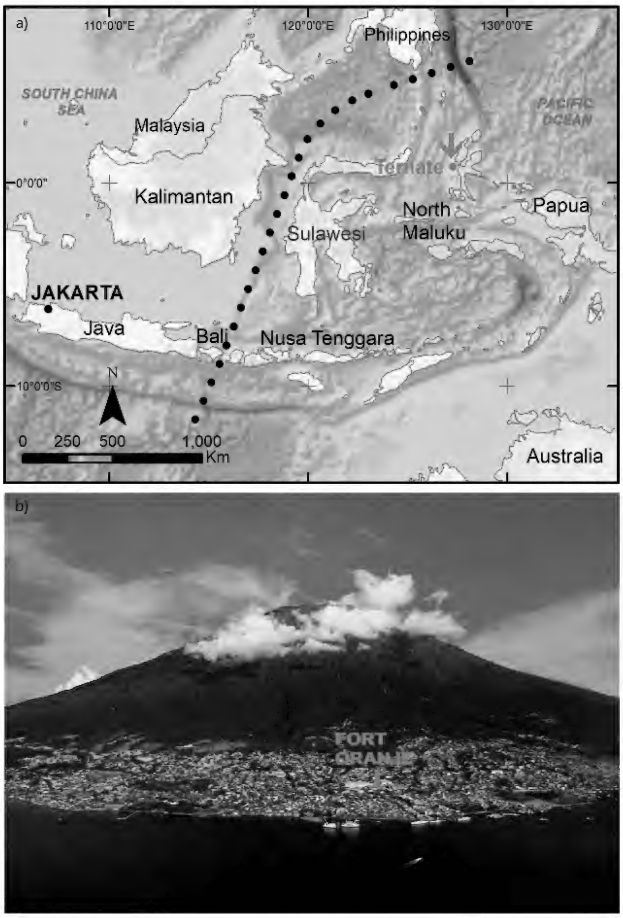

Figure 1. a) Location of Ternate showing the Wallace Line (dotted line; image created using ArcGIS® software by Esri with data from Garmin, USGS and NPS); b) Ternate City and Island seen from the east, dominated by the active volcano Mount Gamalama (Google image).

the Santiong House. The beach in front of Fort Oranje, where the present market stands, is on reclaimed land.

- *In the opposite direction there were no more European houses between me and the mountain*. This confirms that Wallace lived near the edge of the European Quarter. The remains of the northern perimeter wall of that neighbourhood exactly matches the position shown by the 'Master Plan of Fort Oranje' (Reimer 1750). De Clercq (1890) noted that the area directly west of Fort Oranje was a military training ground with no houses. Only at the Oranje Site would there have been no European houses between Wallace's house and the mountain. De Clercq (1890, p. 13) also states that 'since the white walls surrounding the compounds suffer much damage from the continuous rains and most of the inhabitants do not want to replace them with hedges—the walls are a real Old Dutch custom'.
- *Just below my house is the fort, built by the Portuguese, below which there is an open space to the beach*. There is no Portuguese fort near the Oranje or Santiong Sites. Fort Oranje, built by the Dutch in 1607, is just below the Oranje Site and fronted what was then the beach. Supporters of the Santiong House insisted that the remnant walls, which are directly below the Santiong House, were the remains of a Portuguese Fort but it is clear that they are part of the northern boundary wall of the former European Quarter. There is a Portuguese fort, Fort Tolukko, situated north of Fort Oranje. The other Portuguese forts (Kota Janji and Kalamata) are at the southern end of the island, but neither match Wallace's descriptions.
- *Beyond this the native town extends for about a mile to the northeast. About the centre of it is the palace of the Sultan*. The native town is north-northeasterly from both the Oranje and Santiong Sites. The Sultans Palace is about 1.2 km to the north.

Additionally, Wallace (1869, p. 233) presents a floor plan and description of his house with its dimensions. Although not shown, the deep well would have been at the rear of the house. All stone houses in that area were destroyed during the severe earthquake of 1840 (De Clercq 1890, p. 247) and would have had to be rebuilt. It is not known whether the Wallace House was there prior to the earthquake and survived, or if it was reconstructed after 1840.

THE POSSIBLE WALLACE HOUSE SITES

The Sultan's House

The first reference to this traditional house owned by the Sultan's family is a 1986 photograph reproduced by Gardiner *et al.* (2008, p. 16) showing the house in a rather dilapidated condition. The City of Ternate subsequently renovated the house, which they nominated as the official Wallace House. Although an attractive traditional building that continues to receive visitors, it does not meet any of the Wallace criteria or house dimensions.

The Santiong House

According to local residents, a Japanese engineer residing at this house during World War 2 described it as having historical importance (inferring it was the "Wallace House"), but the basis for that claim is unclear. However, a Japanese research team led by Akio Niizuma visited the house in 1980 and 1988 and, relying on local knowledge, used the presence of an old deep well to designate it as the Wallace House (Niizuma 1997, p. 230). At the time only one other well was recognised—this may have been at the Sultan's House. Akio Niizuma communicated this finding to Dr Najib, the then owner of the house, and forwarded him a copy of *The Malay Archipelago* inscribed with his name. Dr Najib passed on this inscription thereby allowing Niizuma's Wallace book to be traced. There is no evidence that previous researchers accessed this book. Professor Marzuki Sangkot, a Wallace scholar, and Syamsil Andili, the mayor of Ternate at that time and a Wallace enthusiast, nominated the Santiong House as the Wallace site at the 2008 Wallacea conference in Makassar (Marzuki & Syamsil 2015). A Tempo magazine article (Hidayat & Nurgianto 2017) gives further background on the Santiong House. Its current dimensions include a 10 m frontage to Jalan Juma Puasa by 15 m next to Lorong A Wallace with an open area at the rear, where the well is situated. In that article

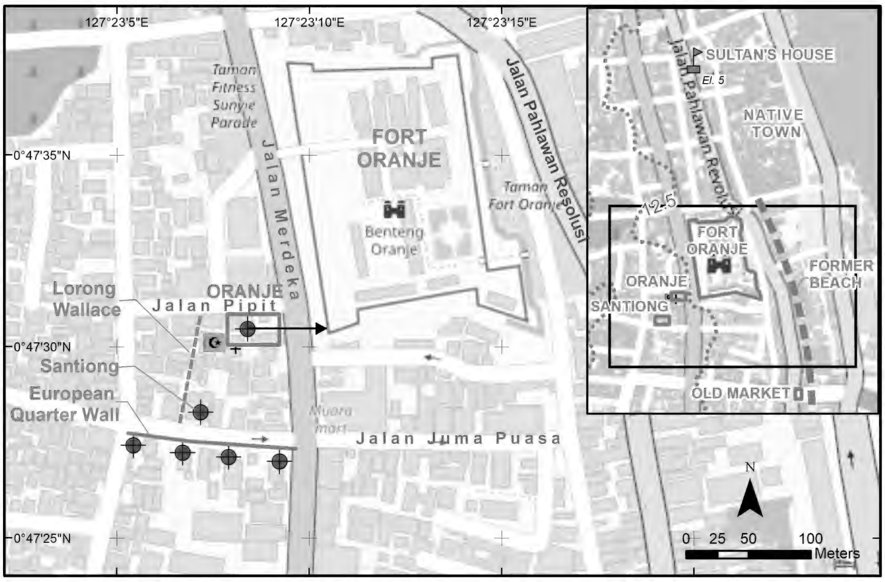

Figure 2. Features described by Wallace (1869) relative to the location of the house he rented in Ternate (superimposed on Google street view map). Also shown are deep wells (blue circles) identified during well survey; remnant wall at European Quarter; line of sight to Fort Oranje from the Oranje site; and the 12.5 m topographic contour.

Maulana Ibrahim of the Faculty of Architecture, Khairun University, Ternate, disputes the Santiong House as the Wallace House, stating that a traditional house has the dimensions of 8 x 15 m whereas the Wallace House was 12 x 12 m.

DEEP WELL SURVEY

The hydrogeology of geologically young active volcanoes such as Mount Gamalama is well understood. This volcano dominates the island of Ternate, rising to 1761 m ASL, with uppermost slopes of about 40° and middle slopes of about 26°, the angle of repose for young volcaniclastics. Active volcanoes such as Mount Gamalama are the principal source of water for the majority of Indonesians, either as surface runoff, springs or groundwater. The average annual rainfall at Ternate City is 2160 mm but is probably closer to 4000 mm at the summit of the volcano. On the upper slopes, the water table is over 100 m deep, but as the elevation drops the water table rises towards to the surface—where the gradient flattens the groundwater discharges as springs around the perimeter of the volcano. Discharge from the volcanic aggregate can be as high as 40% of the rainfall as the high porosity and permeability of the volcaniclastics allow high groundwater recharge. The gradient of the water table at lower elevations is relatively steep and sub-parallel to the ground surface thereby allowing depth to the water table to be predicted from the surface elevations. Deep wells (considered to be >10 m) have only been constructed at elevations above 15 m ASL where the water table is about 5 m ASL. All wells dug by hand could only penetrate one or two metres below the water table before the inflow of water became too great for digging to continue. De Clercq (1890, p. 22) mentioned that most residents along the beach front used shallow brackish wells and were reluctant to construct deeper wells further up the hillside because of the cost—this probably would not have been an issue for the owners in the European Quarter. The survey of old deep wells identified six within the area described by Wallace at elevations above 15 m ASL (Fig. 2). Four of these are aligned approximately 32 m apart within the remnant walls marking the northern boundary of the old European Quarter. The others are at the Santiong House, just to the north of the European Quarter, and at the Oranje Site with the southwestern bastion of Fort Oranje "just below". All six are over 10 m deep with the water uniformly at 28°C and with low salinity. The old well at the Sultan's House, predicted to be no more than 2.5 m deep prior to the survey, is shallow with a measured depth of 2.4 m. Unfortunately, investigation of the well at the Santiong House, estimated to be 12 m deep, was prevented by a concrete cover. A small diameter pipe through the cover was too small for the water-level probe but a depth of 14.8 m was measured using a bolt suspended from a string; seemingly, the string coiled when it reached the bottom as a previous owner suggested the true depth is 13 m. Another old well found during the survey directly south on the opposite side of Jalan Juma Puasa at a slightly lower elevation is 11.9 m deep.

The Oranje Site

Although the deep well at the Oranje Site was covered, the owner opened it for inspection and measurement (Fig. 3a). The walls are composed of volcanic rock bonded with cement-lime (Fig. 3b), similar to the remnants of the European Quarter walls, which date back to about 1750. The walls are closely similar in both design and composition to old shallow wells preserved within Fort Oranje, construction of which commenced in 1607. The well at the Oranje Site is 11.6 m deep, with the water table at 11.0 m. The Oranje Site occupies 850 m^2 with frontages to Jalan Merdeka and Jalan Pipit; the Wallace House would have had three steps leading down from the front veranda to the road, and faced Fort Oranje. Since Wallace's time the land has been subdivided into two. The part facing Fort Oranje (Fig. 4), which is currently vacant land, formerly supported a house facing east towards the fort according to the present owners. This vacant block covers 420 m^2 and is 17.6 x 24.0 m whereas Wallace's house was 12 x 12 m. The well is about 10 m west of where the back veranda would have been. No evidence of the original house remains, but it is hoped that the authorities and the owners will permit an archaeological survey.

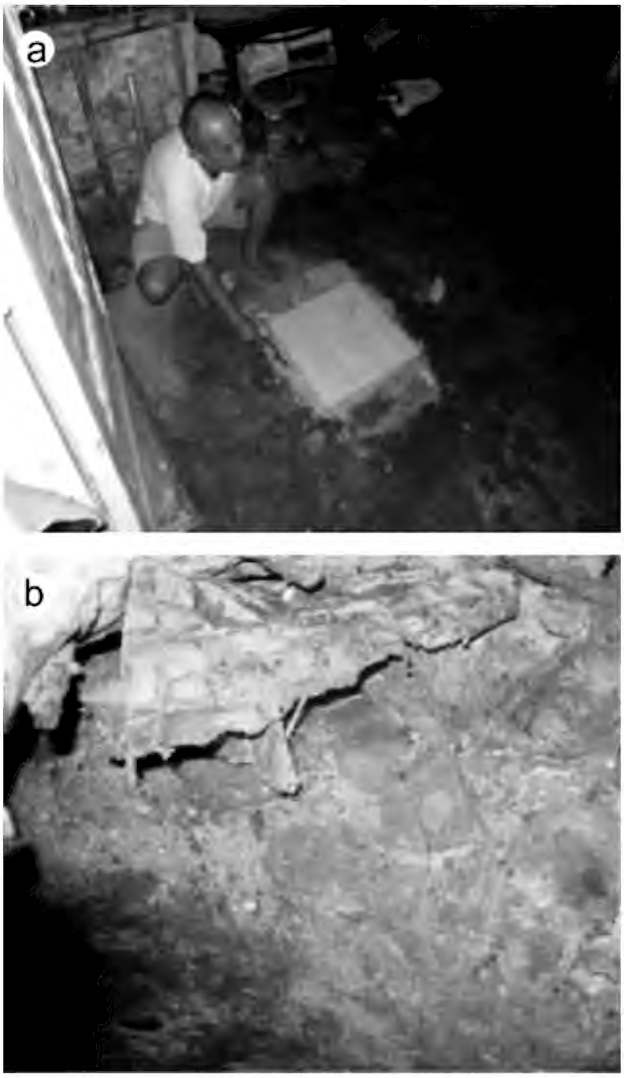

Figure 3. a) Covered deep well inside kitchen of house at Oranje Site prior to opening; b) Wall fabric of deep well at Oranje Site (image from Fiffy Sahib).

DIFFERENTIATION BETWEEN ORANJE AND SANTIONG SITES

George Beccaloni (2012, and in Stammers 2018) recognised the importance of "just below is the fort" while in Ternate acting as adviser during the making of Bill Bailey's Wallace film, *Jungle Hero*, released in 2013. A line of sight drawn eastwards from the front porch of the "Wallace House" at the Oranje Site (Fig. 5) shows that the southwest bastion of the fort is about 60 m away, which qualifies it as being "just below". By comparison, the Santiong House faces south away from the fort, which could only have been seen from the back porch at the time of Wallace, and is 135 m from the fort. The dimensions of the Santiong House do not match the Wallace description whereas the Wallace House would comfortably fit at the Oranje Site.

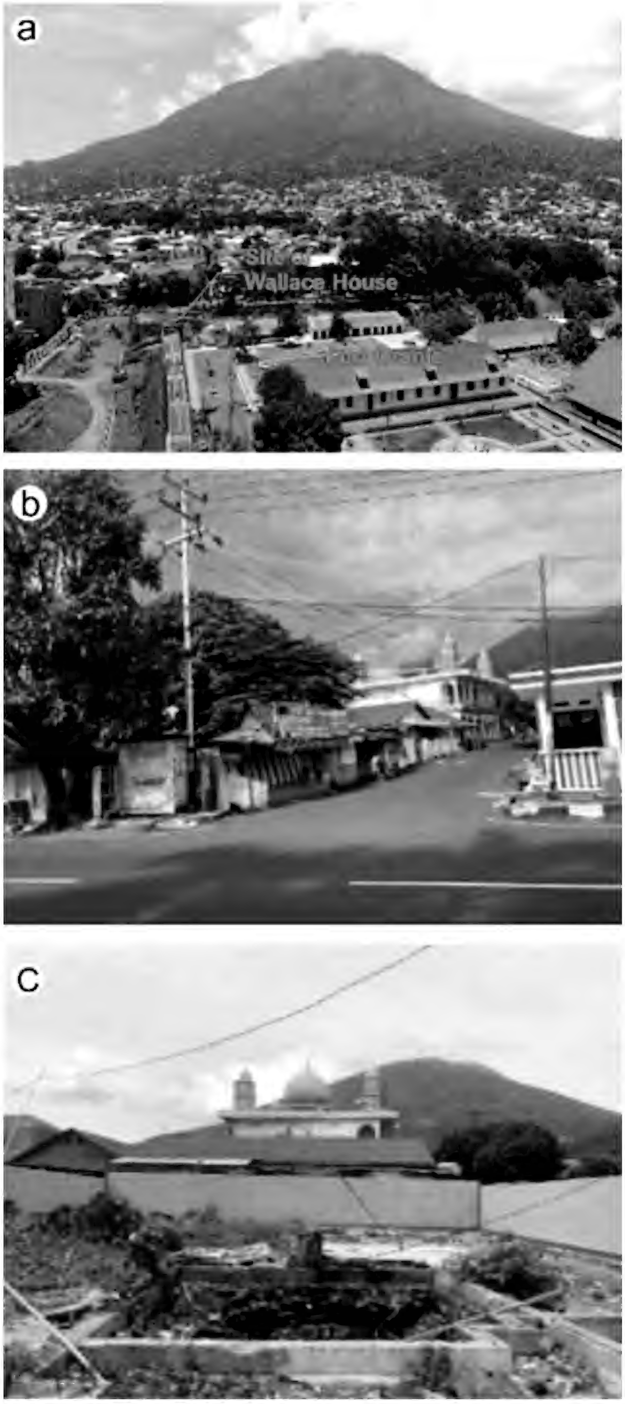

Figure 4. a) The site of the Wallace House, looking west across Fort Oranje to Mt. Gamalama; (image from Sinclair Stammers); b) View from Fort Oranje to the Oranje Site, corner of Jalan Merdeka and Jalan Pipit; c) the site in February 2020 after the vacant land had been cleared and boarded; (image from Krithika Varagur).

CONCLUSIONS

When Wallace despatched his 'Ternate Letter' to Charles Darwin he probably lived at the Oranje Site. The key factor in identifying this site was the discovery of an old deep well. The City of Ternate plans to purchase this site, despite its value having risen considerably since first publicised in late 2019, and then build a replica house conforming to the description and dimensions given by Wallace (1869, p. 313–314) to operate as a museum and biodiversity centre and to help promote tourism.

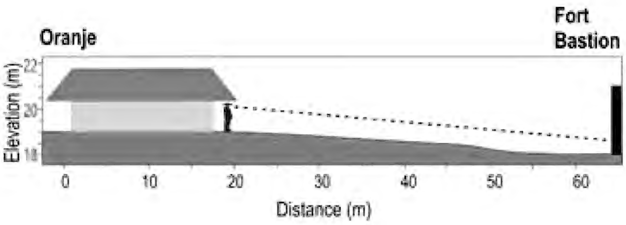

Figure 5. Line of sight to Fort Oranje from Oranje Site.

ACKNOWLEDGEMENTS

The author thanks George Beccaloni who first recognised that the Santiong House had been incorrectly designated as the Wallace House and who, through ongoing updates to *The Alfred Russel Wallace Website*, has contributed greatly to the success of the project. Thanks are also due to Nicholas Hughes who has provided constant support throughout the duration of this research and David Parry for his expert advice on old maps of Ternate. Fiffy Sahib was the key member of the Ternate team facilitating contacts with the local community; Burhan Abdurrahman, the mayor of Ternate, provided unwavering interest; and Rinto Taib, Head of History and Cultural Heritage in the Department of Culture on Ternate, enthusiastically and willingly shared his substantial historical knowledge of Ternate.

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Alfred Russel Wallace –

the man and his work: a review of some recent publications

2019 was the 150th Anniversary of the publication of Alfred Russel Wallace's *The Malay Archipelago*, his most well-known publication, and it is entirely appropriate that this publication, perhaps his most lasting memorial, as well as other aspects of his life and work, should receive careful study at this time. Recent publications have attempted to ensure that Wallace gets his fair share of attention in the debate about the origins of the theory of evolution through natural selection. These have included arguments that there has been a conspiracy to down-play the role of Wallace. Some authors have argued that the letter from Wallace, containing his evolution paper, arrived much earlier than Darwin stated, e.g. in a letter to Charles Lyell dated 18 June 1858 (Burkhardt & Smith 1991), and that he plagiarised Wallace's ideas. This 'conspiracy view' is outlined in several of Roy Davies' publications, some of which go into considerable detail (see, for example, his 2012 paper in the *Linnean Society Biological Journal* with the provocative title: 'How Charles Darwin received Wallace's Ternate Paper 15 days earlier than he claimed'). This conspiracy theory has, however, been answered by van Wyhe & Rookmaaker (2012) with a close analysis of the timing of steamships and postal procedures. Several authors have recently attempted to evaluate Wallace's contribution to the various fields in which he worked: natural history, physical geography, political and social theory, as well as his strange interventions into what some have labelled 'pseudoscience'. Another theme amongst recent publications has been to compare the environment and ecology of south-east Asia as recorded by Wallace with that of today.

The titles of some earlier biographies imply that Wallace played 'second fiddle' to Darwin and was perhaps eclipsed by him; typical is *Darwin's Moon* (Amabel Williams-Ellis 1966). By comparison, *In Darwin's Shadow* Michael Shermer (2002) adopts a psychological approach, but the title clearly suggests that Darwin outshone Wallace. David Lloyd (2012) attempts to stress the importance of Wallace's contribution, and includes a compact biography and summary of his work. Unsurprisingly, the author, who writes from Cardiff, highlights Wallace's Welsh origins. The final words emphasise the paper's message:

> 'The inescapable conclusion is that if Wallace had not attempted to evoke the approval of his hero, but instead had submitted his theory to a journal as sole author, it would not be Darwin but Alfred Russel Wallace who would now be celebrated for our understanding of divergence, speciation and natural selection.'

Although he spent nearly four years in South America (1848–1852), Wallace lost most of his specimens and notes in a fire aboard the vessel that was taking him back to England. Despite this, the publications that followed from his Amazonia explorations were significant.

The Dutch East Indies (as they then were, now Indonesia), which Wallace explored during 1854–1862, had the greatest influence on his subsequent scientific work. *The Malay Archipelago* (1869) is not only a splendid tale of travel, derring-do and adventure but an important scientific survey. Nevertheless, it is not without error, for Wallace was sometimes cavalier on details such as dates and place-names. *The Annotated Malay Archipelago* (2015), edited by John van Wyhe, aims to point out these occasional errors, give the modern scientific names of the organisms mentioned, add details on the identity of some of the persons he met, and sometimes to compare the world of Wallace with that of today. No Wallace scholar should be without this volume, which include Wallace's original woodcuts supplemented by other period colour and monochrome illustrations.

Van Wyhe's (2013) volume, *Dispelling the Darkness: Voyage in the Malay Archipelago and the Discovery of Evolution by Wallace and Darwin*, excellently complements the above book. It briefly summarises Wallace's earlier years, and then provides a detailed itinerary of his Asian voyage, describing the voyage out to Singapore, and through the archipelago. Particularly important is his thorough account of the genesis of the Ternate essay (that set out Wallace's evolutionary hypothesis) and its journey to Darwin's home in Kent, demonstrating beyond reasonable doubt that the arrival date at Downe of 18 June 1858 is accurate and that the suggestion by some that it arrived two weeks earlier is incorrect.

The third of this trinity of works on Wallace's Asian experience is *Alfred Russel Wallace: Letters from the Malay Archipelago*, also first published in 2013, which includes some 88 letters written from (and to) Wallace during this sojourn. This book, edited jointly by John van Wyhe and Kees Rookmaaker, by including letters written by Wallace, unequivocally shows that he was extremely pleased with the handling of his Ternate paper by Lyell and Hooker as a joint presentation to the Linnaean Society alongside Darwin's statement. Many other sources confirm that there was no lingering resentment.

Natural Selection & Beyond by Charles Smith and George Beccaloni, was published in 2008 and aims to cover the entire breadth of Wallace's work. It combines the output of 25 authors. A preface describes his field collecting methods in great detail. The first chapter describes the many houses Wallace lived in, which some have taken as indicating a rather restless life. The remainder of the book is divided into two: 'Part I: In the World of Nature' covers the vast range of Wallace's biological work: his early years as a beetle collector (a trait he had in common with Darwin), on animal coloration, on biogeography and his role as an early conservationist. 'Part II: In the World of Man and Worlds Beyond' discusses the remainder of this great polymath's contribution. Here we meet Wallace the socialist and consider his strange flirtations with the occult, his campaign against vaccination, his interest in astronomy and speculations concerning the possibility of life outside Earth (he was highly doubtful). Wallace was above all

an integrator, and this book argues that the whole of his work shows a belief in *progress* and *improvement*: in life, in society and in the human spirit.

Eleven years later (2019) Charles Smith edited (and contributed extensively to) a comparable work: *An Alfred Russel Wallace Companion*. This has a different set of authors (although there is some overlap), and is perhaps more conceptual: it aims to set the scene in terms of the main thrusts of the Victorian naturalist's work. Chapter headings include 'The early evolution as Wallace as a thinker', 'Wallace, Darwin and natural selection' and 'Wallace as social critic, sociologist and societal "prophet"'. Other sections discuss Wallace's approach to physical geography, biogeography and conservation biology. A final chapter gives an account of 'Wallace and extraterrestrial life'. The book provides an up-to-date overview of the products of Wallace's intellect, and shows something of the relationships that existed between the different themes displayed in his work.

It is sometimes argued that Charles Darwin moved from 'natural theology' to 'natural selection'. Natural theology, as expounded by William Paley (whose works Darwin read while a student at Cambridge), sought to demonstrate the existence of God, and gain some insight into the mind of the Creator through an understanding of the complexity, beauty and diversity of the natural world. Although Darwin found Paley's work of great interest, and his examples useful, he obviously later argued that natural processes were responsible for the nature and diversity of organisms. Recently, Michael Flannery's (2018) *Nature's Prophet: Alfred Russel Wallace and his Evolution from Natural Selection to Natural Theology* attempts to show how Wallace moved, in the course of his life and work, in the opposite direction. Flannery states:

> 'The argument is essentially this: Wallace's understanding of the natural and metaphysical worlds essentially became one – an integrated whole of scientific, social, political and scientific thought – through the latter part of his life, forming a revised natural theology over the moribund special creation of William Paley.'

There were, from the outset, differences in how Darwin and Wallace understood evolution, and these became more pronounced as the years went by. Chapter three of Flannery's book documents the 'parting of the ways'. Wallace maintained that although natural selection could explain many aspects of the form of organisms (including humans), he believed that 'man's moral sense', and certain other aspects of the living world could not. He maintained that there existed a 'creative power' and that there was a *directionality* in evolution; whereas natural selection emphasised random processes. At this, as he put it himself, Darwin 'groaned'. Flannery thus interprets Wallace's development as having moved from a point quite close to Darwin's natural selection towards natural theology. Wallace, furthermore, perceived the role of design in the whole cosmos. Humanity could be seen as the 'goal' or end-point of evolution both organic and cosmic (chapter 7): hence Wallace's belief in the extreme unlikelihood of intelligent life existing elsewhere in the universe. Flannery's approach will not please all.

Several authors have attempted to 'follow in the footsteps of' both Wallace and Darwin: these modern travellers and scientists have compared the places visited by HMS *Beagle*, 1831–1836, with the same localities today, or to contrast the East Indies of Wallace's sojourn there with the islands of Indonesia as they now are. A well-received example of the latter is Tim Severin's (1998) *The Spice Islands Voyage: In Search of Wallace*: this provides a 'good read' and some local colour.

Recent publications have removed Wallace from the 'shadow' of Darwin, and allowed his intellect to illuminate the world in its own distinctive manner.

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PATRICK ARMSTRONG

University of Western Australia

✉ *parmstro@highway1.biz*

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Ammobaculites (Foraminifera): living fossils in southern Western Australian estuaries

DAVID W. HAIG *

Oceans Graduate School, The University of Western Australia, 35 Stirling Highway, WA 6009, Australia

* *Corresponding author: ✉ david.haig@uwa.edu.au*

Abstract

Ammobaculites assemblages are recorded from five localities selected during reconnaissance sampling of shallow-water mud in the hyposaline reaches of Wellstead Estuary, Kalgan River, Frankland River, Walpole Inlet and Hardy Inlet. The aim of the study was to: (1) find potential living populations that in future could be the subject of biological, including molecular, investigations, and (2) describe the morphological variation in the recovered assemblages. In the geological record, *Ammobaculites* is one of the longest ranging multichambered genera within the Phylum Foraminifera, and is common in shallow-marine mudstone facies of Gondwanan/ Australian interior basins of the Late Paleozoic and Mesozoic. The southern Western Australian estuarine *Ammobaculites* are compared to five main morphotypes recognized in this genus among the global estuarine fauna. The most common form here is referred to *Ammobaculites* sp. ex. gr. *A. exiguus*; and another species, although related to one of the morphotype groups, does not appear to have close counterparts elsewhere. Species confirmation and comparisons to morphologically close forms in eastern Australian and on other continents must await future rDNA sequence study. The modern *Ammobaculites* are also compared to Australian continental fossil assemblages from the Permian, Triassic and Cretaceous, in which there are close morphological analogues. The modern types are living fossils whose future study could contribute to resolution of questions concerning the geological longevity of the genus, the morphological and potential genetic conservatism within the genus, and how such similar morphotypes that thrive in isolated ephemeral mud in marginal-marine environments can disperse across regions and continents in both space and time.

KEYWORDS: Organic-cemented agglutinated foraminifers, Wellstead Estuary, Kalgan River, Frankland River, Walpole Inlet, Hardy Inlet, Permian, Triassic, Cretaceous

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INTRODUCTION

Foraminifera are present in almost all marine environments (Murray 1991) and also have a long evolutionary history (Pawlowski *et al*. 2003) that is represented in fossil assemblages throughout the Phanerozoic (see review by Haig *et al*. 2018, on the Western Australian record). The oldest preserved foraminifers belong to organic-cemented agglutinated groups that build their tests mainly from silicate grains. These conservative groups display minor changes in morphology over long periods of time (Haig & McCartain, 2010). Some genera that are present in modern Western Australian estuaries have close morphological counterparts that lived in Permian to Cretaceous restricted estuarine-like interior seas across Australia (Haig *et al*. 2018), and elsewhere extending back 350 million years to the Early Carboniferous (Mississippian). The genera include *Ammobaculites* Cushman selected by Haig (1979, 2004) to characterize foraminiferal assemblages of the ancient estuarine-like interior seas as the *Ammobaculites* Association.

To understand better the palaeoecology of fossil *Ammobaculites* and the implications this has for interpreting marine conditions within ancient interior continental basins as far back as the Late Paleozoic, it is important to gain a greater knowledge of modern *Ammobaculites* in estuarine situations. This includes identifying the degree of morphological variation within a species; using molecular techniques to assist in species recognition and relationships among close morphotypes; and gaining better insights into the biology of the species (especially microhabitat preference, food sources, reproduction cycles, test construction, selectivity of agglutinated material, and means of dispersal). Such studies require considerable time and inputs from more than one laboratory. A prerequisite for these studies is locating suitable assemblages in modern estuaries that are easily accessible and are likely to contain numerous living representatives.

In a reconnaissance of estuaries along the southern coast of Western Australia during September 2019 and February 2020, abundant to common *Ammobaculites* were found at five sites (Fig. 1; Appendix 1). The aim of this paper is to document the assemblages found at these localities. As the first step to a better understanding of *Ammobaculites* in this region, the morphological variation among tests is recorded and illustrated, and possible specific relationships are discussed that could be tested by molecular techniques. Morphotypes are compared with those found among fossil assemblages and the reasons for any conservatism in morphology

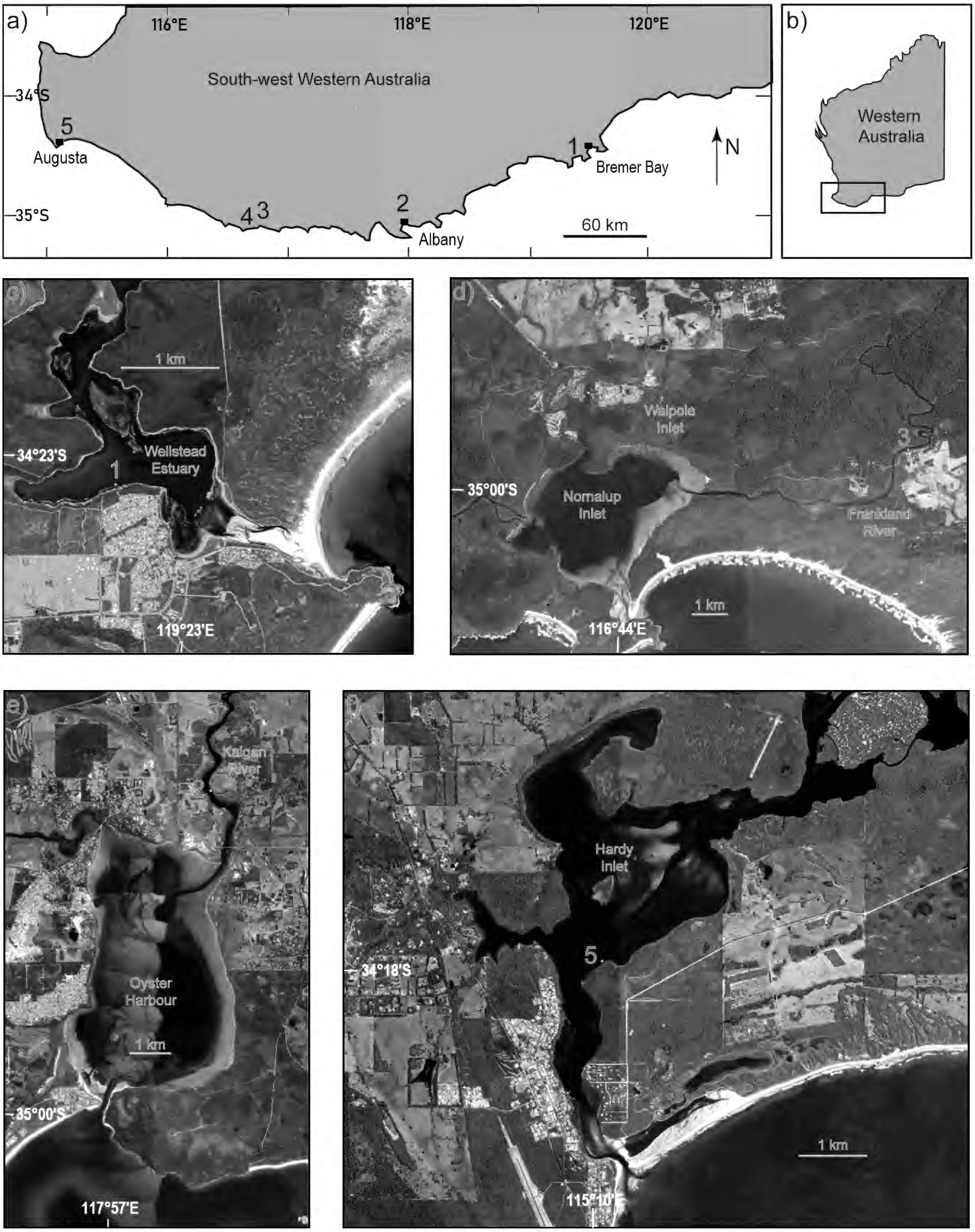

Figure 1. Google Earth images of sampled localities in (c) Wellstead Estuary, Bremer Bay, locality 1; (d) Frankland River, locality 3, and Walpole Inlet, locality 4; (e) Kalgan River, locality 2; and (f) Hardy Inlet, locality 5.

are canvassed. Future biological research, especially into microhabitat preference and means of dispersal, could support or negate such contentions.

SIGNIFICANCE OF *AMMOBACULITES*

Cushman (1910) established the genus *Ammobaculites* based on the agglutinated foraminifer *Spirolina agglutinans* d'Orbigny (1846) from the Middle Miocene, Badenian, of the Vienna Basin. D'Orbigny (1846, p. 137, 138, pl. 7, figs 10–12) did not designate a type specimen for *S. agglutinans*, but illustrated line drawings of a test in lateral, peripheral and terminal (apertural) views. These show a specimen, about 1 mm long, including a broad involute coil with 4.5 chambers exposed, and a straight uniserial final stage, composed of three almost cylindrical chambers, that is positioned excentrically on the initial coil. The aperture is illustrated and described as an oblong opening. As indicated by Kaminski & Gradstein (2020), the lectotype chosen by Papp & Schmid (1985, p. 54, pl. 45, figs 7, 9) is valid rather than that selected by Loeblich & Tappan (1964, p. C241, fig. 151, nos 6a, b). The lectotype has features close to d'Orbigny's (1846) illustrated specimen apart from an additional uniserial chamber and a partly obscured aperture. With the provision of a lectotype for the type species, the name "*Ammobaculites*" is firmly established, but the concept of this genus and its other species is less than settled. According to Papp & Schmid (1985), *Ammobaculites agglutinans* comes from a deep-water calcareous clay facies where it is extremely rare.

In many descriptions of *Ammobaculites*, little information is given on wall structure, and in particular the type of cement that agglutinates the grains forming the test although this may be a critical character in suprageneric classification. Agglutinated foraminifers fall into two main groups based on cement (Loeblich & Tappan 1989) as outlined below.

(1) Organic (glycosaminoglycan)-cemented types (Hedley 1963; Towe 1967; Mendelson 1982; Langer 1992; Allen *et al*. 2000) usually agglutinate silicate grains (mainly quartz, but sometimes also an abundance of other silicate minerals as shown, for example, by Armynot du Châtelet *et al*. 2013). Occasionally carbonate fragments are included in the test where these are present in the substrate, as in the type specimens of *Ammobaculites agglutinans* (see Kaminski & Gradstein 2020).

(2) Carbonate-cemented species contain either calcite or aragonite as the cement (Murray 1973, Bender & Hemleben 1988, Robert & Murray 1995).

Among the phylogenetic relationships charted by Pawlowski *et al*. (2003, fig. 1) the few species analysed that belong to multichambered organic-cemented agglutinated taxa (viz. species of *Arenoparella*, *Haplophragmoides*, *Reophax*, *Spiroplectammina* and *Trochammina*) cluster together. These are distant from the carbonate-cemented agglutinated cluster of *Siphoniferoides*, *Textularia* and *Bigenerina*. The carbonate-cemented types probably had their origin among calcareous microgranular forms with single-layered walls that belonged to primitive Fusulinata in the Upper Devonian and Lower Carboniferous, as suggested by the works of Piller (1990) and Rigaud *et al*. (2015).

The organic-cemented agglutinated types had a far longer evolutionary history than the carbonate-agglutinated foraminifers, and are known at least from the Early Cambrian (e.g. undisputed unilocular types described from West Africa by Culver 1991, 1994). Undisputed multilocular agglutinated foraminifers with organic cement (viz. *Reophax*) are known from at least the Middle Ordovician (Gutschick 1986). Although "*Ammobaculites*-like" morphotypes were described by Scott *et al*. (2003) from the Cambrian of Nova Scotia, their chamber arrangements are unclear and the identifications are unconvincing. Illustrated specimens identified as *Ammobaculites* from the Silurian by Kaminski & Perdana (2017) have ambiguous chambers and from the Devonian by Holcová & Slavik (2013) have uncertain wall composition, and require further evaluation. *Ammobaculites* was well estabished in shallow interior-sea faunas by the Mississippian (Early Carboniferous; Haig & McCartain 2010, appendix 3).

Ammobaculites is not included in Pawlowski & Holzmann's (2020) molecular database of foraminifers. As discussed by Haig & McCartain (2010, p. 375) it belongs within the Family Haplophragmoididae. The basic morphotype of initial coil followed by uniserial erect stage is also represented in unrelated groups of foraminifers: for example, *Endotebanella* and *Endotriadella* (see Vachard *et al*. 1994) among the Fusulinata; *Coscinospira, Monalysidium* and *Spirolina* (see Loeblich & Tappan 1987) among the Miliolata; and *Marginulinopsis* (see Loeblich & Tappan 1987) among the Nodosariata.

On continental platforms, carbonate-cemented agglutinated foraminifers are restricted to normal marine and hypersaline shelf seas (Murray 1973). Although organic-cemented agglutinated species are present here, their frequencies are usually much lower than calcareous foraminifers. The organic-cemented types become abundant in the hyposaline reaches of shallow estuaries and interior seas. In present-day environments, *Ammobaculites* assemblages are most common in estuarine organic-rich mud facies (Ellison 1972, Murray 1991), although species are also present on continental shelves and in the deep sea, albeit at much lower frequencies (Murray 1991, Holbourn *et al*. 2013, Kaminski & Gradstein 2020). Among the estuarine *Ammobaculites* reported globally, five broad morphotypes are recognized (Table 1). The type species, *A. agglutinans*, typifies morphotype A. From Australian estuaries (Tables 2, 3), six global species names have been used in identifications together with two new species based on local faunas, including one from Western Australia. Most of the published records of *Ammobaculites* in Australian estuaries contain few illustrations of the morphotypes present and variability is often poorly described.

Shallow interior seas that flooded over the Eastern Gondwanan–Australian continent from about 300 to 80 Ma contain abundant *Ammobaculites* faunas in organic-rich mudstone facies. The oldest *Ammobaculites* assemblages here are Permian (Crespin & Parr 1941; Parr 1942; Crespin 1945, 1947, 1958; Belford 1962, 1968, Ludbrook 1967; Scheibnerová 1982; Foster *et al*. 1985,

Table 1

List of *Ammobaculites* species names used in identification of global estuarine faunas (forms later transferred to *Ammotium* are not included). The species are assigned to broad morphotypes (A–E) to facilitate comparisons with the Western Australia *Ammobaculites*.

A. Species with an initial broad involute planispiral coil and a later cylindrical uniserial stage of lesser diameter positioned excentrically above coil.

Type species of *Ammobaculites*:
Spirolina agglutinans d'Orbigny, 1846, p. 137, pl. 7, figs. 10–12. [Lectotype: Papp & Schmid, 1985, p. 54, pl. 45, figs. 7, 9; plus one other specimen from type assemblage pl. 45, fig. 8]: Middle Miocene, Vienna Basin, Austria.
Other species:
Ammobaculites? *barwonensis* Collins 1974, p. 9, pl. 1, figs 3a, b (holotype): Barwon estuary (only at type locality 56-C9, "muddy sand, right bank of Barwon River on N. boundary of Area 56" ~ 38.2647°S, 144.5083°E).
Ammobaculites exiguus Cushman & Bronnimann 1948, p. 38, pl. 7, figs 7a, b (holotype), 8 (paratype): Shoreline (0–3 m), Gulf of Paria, Trinidad.
Ammobaculites formosensis Nakamura 1937, p. 14, p. 133, pl. 10, figs 1a, b: Neogene (? Pliocene), Taiwan. [Fide Ellis & Messina 1945 et seq.]
Ammobaculites neusensis Grossman 1967, p. 49, pl. 1, figs 1, 6: Neuse, Pamlico and Punga rivers and Pamlico Sound, North Carolina.
Ammobaculites pamlicoensis Grossman 1967, p. 48, pl. 1, figs 12, 16, 17: Neuse, Pamlico and Punga rivers and Pamlico Sound, North Carolina.

B. Species with cylindrical uniserial portion positioned centrally above initial involute planispiral coil
Ammobaculites balkwilli Haynes 1973, p. 25–27, pl. 2, figs 2, 3; pl. 29, figs 5, 6; text-fig. 4, nos 1 (holotype), 2–5 (paratypes): Dovey Marshes, Cardigan Bay, Wales.
Ammobaculites josephi Acosta 1940, p. 271, pl. 49, figs 2 (paratype), 7 and 10 (holotype): Gulf of Santa Maria, Cuba [Fide Ellis & Messina 1945 et seq.]
Ammobaculites villosus Saidova 1975, p. 93, pl. 25, fig. 12 (holotype): 156 m water depth off west coast of South Island, New Zealand [fide Ellis & Messina 1945 et seq.]

C. Species with broad initial involute coil and excentric variably compressed and slightly to distinctly flabelliform uniserial stage, with elongate terminal aperture.
Ammobaculites amarus Hada 1957, p. 30, 31, text-figs. 10a–d: Hijirippu and Mochirippu brackish-water lakes, southeast Pacofoc coast of Hokkaido.
Ammobaculites dilatatus Cushman & Bronnimann 1948, p. 39, pl. 7, figs. 10a, b (holotype, 11 (paratype): Shoreline (0–3 m), Gulf of Paria, Trinidad.
Ammobaculites directus Cushman & Bronnimann 1948, p. 38, pl. 7, figs 3a, b (holotype), 4 (paratype): Shoreline (0–3 m), Gulf of Paria, Trinidad.
Ammobaculites diversus Cushman & Bronnimann 1948, p. 38, pl. 7, figs 5a, b (holotype), 6 (paratype): Shoreline (0–3 m), Gulf of Paria, Trinidad.
Ammobaculites exilis Cushman & Bronnimann 1948, p. 39, pl. 7, figs 9a, b (holotype): Shoreline (0–3 m), Gulf of Paria, Trinidad.
Lituola (*Haplophragmium*) *foliaceum* Brady 1881, p. 50. [Brady 1881 p. 45 inferred that figures of this species were to be included in a larger monograph. This was published as *Haplophragmium foliaceum*; Brady 1884, p. 304, 305, pl. 33, figs. 20–25; deep sea, Atlantic, Pacific, Southern oceans. [Placed in *Ammomarginulina* by Barker 1960, p. 68; and to Eratidus by Jones 1994, p. 40; this is the type species of *Eratidus* Saidova 1975]
Ammobaculites morenoi Acosta 1940, p. 272, pl. 49, figs 1 (paratype), 3 and 8 (holotype): Port of Santa Maria, Cuba [Fide Ellis & Messina 1945 et seq.]

D. Species with partially evolute initial coil and cylindrical to slightly compressed uniserial stage excentric on coil
Ammobaculites crassus Warren 1957, p. 32, pl. 3, figs 5 (holotype), 6–7 (paratype): [with slightly oblique sutures; ? transitional to *Ammotium fragile* Warren 1957, pl. 1, figs 14 (paratype), 15 (holotype)]: interconnected lakes in Louisiana coastal marshlands.
Ammobaculites subcatenulatus Warren 1957, p. 32, pl. 3, figs 11 (holotype), 12–13 (paratype): interconnected lakes in Louisiana coastal marshlands.

E. Species with broad planispiral coil, and only slight development of a compressed excentric uniserial stage
Ammobaculites howelli Acosta 1940, p. 273, pl. 49, fig. 11 (holotype): Port of Santa Maria, Cuba [Fide Ellis & Messina 1945 et seq.]

Conkin & Conkin 1993; Palmieri 1993, 1994; Haig 2003, 2004, 2018; Dixon & Haig 2004; Haig *et al*. 2017, appendices 11, 13, 15, 17, 19; Haig & Mory 2016). Triassic *Ammobaculites* species have been described (Heath & Apthorpe 1986; Apthorpe 2003; Haig & McCartain 2010) from mudstone facies in axial basins of the East Gondwana interior rift basins discussed by Haig *et al*. (2018) and the Papuan Basin (Kristan-Tollmann 1988, 1990). No *Ammobaculites* have been described from the Jurassic of Australia because few foraminiferal studies have been published on the marine Jurassic that is confined mainly to the New Guinea margin, and the East Gondwana Interior Rift and successor basins. A broad representation of the genus is present in mid-Cretaceous marine mudstone facies that flooded vast areas of the Australian continent (Crespin 1944, 1953, 1963; Taylor 1964; Ludbrook 1966; Scheibnerova 1976; Haig & Barnbaum 1978; Haig 1980, 1981, 2004, 2005; Jones & Wonders 1992; Haig & Lynch 1993; McLoughlin *et al*. 1995; Holbourn & Kaminski 1997; Campbell & Haig 1999; Howe *et al*. 2000; Taylor & Haig 2001; Dixon *et al* 2003; Haig *et al*. 2004; Stilwell *et al*. 2012).

Table 2

Ammobaculites previously illustrated from Western Australian estuaries and inlets.

Ammobaculites agglutinans (d'Orbigny)	McKenzie 1962, p. 119, pl. 1, fig. 4; Oyster Harbour and lower King River. Quilty 1977, p. 89, fig. 10; Hardy Inlet, lower Blackwood River. Quilty & Hosie 2006, pl. 1, fig. 1; Swan River. Melville Water.
Ammobaculites exiguus (Cushman & Bronnimann)	Ostrognay & Haig 2012, fig. 5, nos. 13, 20; Collie, Murray, Serpentine rivers.
Ammobaculites villosus Saidova	Revets 2000, pl. 1, figs. 2–3; Leschenault Inlet.
Ammobaculites yardiensis Parker	Parker 2009, p. 13, figs. 10a–h, 11a–d; near-shore lagoon, Mangrove Bay, Ningaloo Reef.
Ammobaculites sp. of Quilty 1977	Quilty 1977, p. 89, fig. 11; Hardy Inlet, lower Blackwood River.
Ammobaculites sp. of Revets 2000	Revets 2000, pl. 1, fig. 1;Leschenault Inlet.

Table 3

Illustrated records of *Ammobaculites* and some related morphotypes published from elsewhere in Australia with species nomenclature as originally used.

Ammobaculites exiguus (Cushman & Bronnimann)	Bell 1978, p. 134–135, fig. 4; Limeburners Bay, Victoria. Bell 1996, pl. 1, fig. b; River Tamar, Tasmania. Bell & Drury 1992; fig. 4.10; Mallacoota Inlet, Victoria. Strotz 2003, p. 169, pl. 1, fig. 5; Tuross Estuary and Coila Lake, New South Wales. Strotz 2012, fig. 4(nos. 5–6b), Appendix B, p. 4, 5; St Georges Basin, New South Wales. Strotz 2015, fig. 3E; Smiths Lake, New South Wales.
Ammobaculites barwonensis Collins	Collins 1974, p. 9, pl. 1, figs. 3a, b (sp. nov. as *Ammobaculites*?); Barwon River estuary, one locality. Apthorpe 1980, p. 225, pl. 28, figs 4, 5, 10–13; Gippsland Lakes, Victoria. Bell & Drury 1992, figs. 4.7–4.9; Mallacoota Inlet, Victoria. Bell, 1995, p. 229, fig. 2.2; Lower Barwon River and Lake Connewarre, Victoria. Bell 1996, pl. 1, fig. k; River Tamar, Tasmania. Cann et al. 2000, pl. 1, figs. f, g; northern Spencer Gulf, South Australia. Strotz 2003, p. 169, pl. 1, figs. 6, 7; Tuross Estuary and Coila Lake, New South Wales.
Simobaculites barwonensis (Collins)	Strotz 2012, fig. 4, nos. 7a, b, Appendix B, p. 5, 6; St Georges Basin, New South Wales. Strotz 2015, fig. 3F; Smiths Lake, New South Wales.
Ammobaculites reophaciformis Cushman	Cann et al. 1988, figs. 9a, b; Gulf St. Vincent, South Australia (possibly the agglutinated miliolid *Nubeculina advena* Cushman 1924, p. 53, pl. 19, figs. 1–4). Cann et al. 2000, pl. 1, figs. c–e; hypersaline estuary, Far Northern Spencer Gulf, South Australia.
Ammobaculites agglutinans (d'Orbigny)	Apthorpe 1980, pl. 28, fig. 9; Gippsland Lakes, Victoria. Yassini & Jones 1989, p. 255, Fig. 10, no. 5; Lake Illawarra, New South Wales. Yassini & Jones 1995, p. 70. 71, figs. 46–48, 50; "coastal lagoons and muddy facies of the inner shelf", south-eastern Australia; specific localities not given.
Ammobaculites subcatenulatus Warren	Albani 1978, p. 364, 365, fig. 6E; Broken Bay estuary, New South Wales. Yassini & Jones 1995, p. 71, figs. 44, 45; "strictly coastal lagoons", south-eastern Australia; specific localities not given.
Ammobaculites foliaceus (Brady)	Albani 1978, p. 364, described but not figured; Broken Bay estuary, New South Wales. Yassini & Jones 1989, p. 255, fig. 10, no. 4; Lake Illawarra, New South Wales. Yassini & Jones 1995, p. 71, figs. 51–53; "coastal lagoons and muddy facies of the inner shelf", south-eastern Australia; specific localities not given.
Ammobaculites sp. of Yassini & Jones, 1989	Yassini & Jones 1989, p. 255, fig. 10, no. 6; Lake Illawarra, New South Wales.

Fossil *Ammobaculites* are most common in mud facies of the large interior seas of the Cretaceous (Aptian–Albian) and the shallow marginal-rift seas of the East Gondwana interior rift system in the Western Australia Permian (Haig *et al*. 2017, 2018) and coeval shallow-water basins in eastern Australia (Crespin 1958; Palmieri 1994). As indicated by Haig (1979, 2003, 2004) the interior seas had estuarine-like water conditions with periods of hyposalinity and water-column stratification. The foraminiferal assemblages in these facies were characterized as the *Ammobaculites* Association by Haig (1979, 2004) who recognized equivalents in the vast interior basins of North America (particularly Mississippian and Cretaceous) and Western Siberia (Cretaceous). In contrast to the fossil assemblages from the estuarine-like Australian interior-seas, *Ammobaculites* species are a rare component of foraminiferal assemblages in the more open-marine

mud facies of the Permian and Triassic axial basins in the East Gondwana Interior Rift, and in the open-marine parts of the continental margin basins of the Cretaceous. These areas are characterized by carbonate-cemented agglutinated foraminifers and greater diversity in the overall foraminiferal fauna. The broad pattern of the fossil distributions parallels that noted by Murray (1973) for modern assemblages, except there are fewer large shallow interior seas in humid climatic belts at present than during some intervals in the past when global sea-level was higher and continents were in different tectonic configurations.

LOCALITY DETAILS OF STUDIED ASSEMBLAGES

Studied assemblages of *Ammobaculites* were selected from one site each in five different estuaries/inlets (Fig. 1, Appendix 1). Samples of dark mud or sandy mud were collected using a small pipe dredge designed to scrape a veneer of sediment from the estuarine floor. The dredge was deployed from the shoreline or from a kayak or dinghy. Samples of the mud were washed over a 125-μm mesh sieve and the residue dried for inspection under a stereomicroscope. Images of representative specimens were taken in reflected light using focus stacking and rendering techniques.

All samples were from estuaries or connected rivers well away from the estuarine mouths. No evidence was observed of reworked foraminifers from mid-Holocene highstand deposits (up to ~ 2 m above present sea-level; Baker *et al*. 2001) that are common in the lower reaches of Western Australian estuaries, or from tests derived from the present-day to Pleistocene wind-blown coastal sand dunes in the region. The samples were not immersed in rose-bengal to detect living specimens because staining of protoplasm within the opaque thick agglutinated tests of genera such as *Ammobaculites* is difficult to observe. Living specimens will be found most easily by observing collected mud in aquaria. The colour and preservation of the tests recovered during this study, all with brown organic material incorporated in their walls, suggests that these were either alive or recently dead.

Of the five estuaries/inlets sampled (Appendix 1), the only previous record of foraminifers, including *Ammobaculites*, is from Hardy Inlet (Quilty 1977). McKenzie (1962) recorded the distribution of foraminifers, including rare *Ammobaculites*, in Oyster Harbour into which the Kalgan River flows (Fig. 1e). Comprehensive sampling has not been done at the other sites.

1. Wellstead Estuary

Wellstead Estuary at the mouth of the Bremer River (Fig. 1c) is often closed by an extensive sand bar for many years (as shown in the 2018 Google Earth image, Fig. 1c), and at other times it is open to incursions of normal-salinity sea water. The salinity is highly variable depending on closure of the estuary and seasonal rainfall conditions in the small catchment (Brearley 2005). At the time of collection of the studied assemblage in February 2020, the estuary mouth was closed and water levels within the estuarine basin were very low, much less than the normal 1m water depth. The studied sample (Appendix 1) was taken from the edge of a modern serpulid reef that parallels the shore about 30 m from the shoreline. The water depth at the site was about 10 cm and the substrate consisted of black organic-rich mud. Besides the foraminifers, other components of the washed sand residue from the mud were abundant ostracods, fragments of serpulid tubes, rare bulbous gastropods, rare charophytes, very rare thin-walled bryozoans, and abundant faecal pellets. Salinity was not measured. This site is about 2.5 km from the river mouth, when it is open. In early summer after a winter influx of freshwater and opening of the river mouth it would have salinities approaching normal-marine conditions in contrast to hypersaline conditions (up to 70 psu) when the estuary mouth is closed and water levels are low due to dry conditions (Brearley 2005).

2. Kalgan River

The Kalgan River flows into Oyster Harbour (Fig. 1e) and is microtidal in the reach of the river that includes the studied assemblage (Brearley 2005). At the collecting site (2 on Fig. 1e; Appendix 1) the salinity was 33 psu during an interval of very low rainfall for the region. Under normal weather conditions the salinity would be lower just after winter rains but with marked seasonal changes through the year (Brearley 2005). The sand fraction of the studied mud sample is mainly quartz. Rare gastropod and bivalves together with some indeterminant mollusc debris are also present.

3. Frankland River

The Frankland River drains some of the highest rainfall parts of southern Western Australia (McFarlane *et al*. 2020) and discharges a high volume of fresh water, especially in winter (Brearley 2005). It drains into the large Nornalup Inlet, which has a narrow permanent opening to the sea (Fig. 1d). The studied *Ammobaculites* assemblage comes from muddy sand facies at site 3 about 6.3 km upstream from the mouth of the river into Nornalup Inlet (Table 1). Salinity at the time of collection was 5 psu. The sand fraction of the sediment is mainly quartz but also includes bivalves and gastropods.

4. Walpole Inlet

The small, shallow Walpole Inlet situated at the north-west edge of Nornalup Inlet (Fig. 1d) has only a small local-river input and a salinity (15 psu) higher than the Frankland River (Table 1). The studied assemblage comes from near the shore in the restricted northern part of the inlet. The sand fraction of the mud contains mainly quartz, but also includes large centric diatom frustules and fragments of bivalves and gastropods.

5. Hardy Inlet

Hardy Inlet (Fig. 1f) is the estuary for the Blackwood River and receives the largest volume of freshwater compared to the input into any of the other south coast estuaries because of a high-rainfall hinterland (Brearley 2005; McFarlane *et al*. 2020). Salinity changes seasonally with the greatest influx of freshwater during winter, and with a saltwater bottom wedge advancing up the lower estuary in summer. The studied assemblage was

collected in September 2019 (Appendix 1). No salinity measurement was made at the time of collection. Salinity profiles for April (early Autumn), May (late Autumn), June (Winter) and October (Spring) 1974 presented by Brearley (2005) suggest that at this shallow-water site salinity is probably variably hyposaline throughout the year. The sand fraction of the studied sediment sample consists mainly of quartz. Bivalve fragments are rare.

AMMOBACULITES ASSEMBLAGES

Illustrations of the five assemblages discussed here (Figs 2–6) show considerable variability within each assemblage and among assemblages and highlight difficulties in making taxonomic discrimination based solely on test morphology. Some the variation can be attributed to different growth stages of individuals. Other aspects of difference are due to the types and grain sizes of particles used in construction of the test. There also may be different generations, reflected in morphology, in the complex reproductive cycles of species present. Measurements based on the illustrated specimens also show the variability present (Table 4). Broad morphotypes (A–E) recognized among global estuarine *Ammobaculites* (Table 1) are used here in initial designation of the specimens found in the south-coast estuaries.

1. Wellstead Estuary

Almost all of the specimens of *Ammobaculites* found at site 1 (Fig. 2) belong to global morphotype A (Table 1) that is characterised by an erect uniserial stage positioned excentrically above a broad involute planispiral initial stage. The degree of excentricity varies between extremes as illustrated by the specimen shown in Figure 2o (extreme morphotype A) and tests shown in Figures 2f, l and r (which approach morphotype B). Specimens with very limited development of a uniserial stage (Fig. 2a–c) are regarded as juveniles based on the diameter of the planispiral coil being within the range of other specimens (Table 4).

Chambers in the initial coil are obscure with sutures mainly flush or slightly depressed. The last whorl has 6–7 chambers; earlier whorls are hidden. The coil has a consistent narrow and moderately deep umbilicus. In some tests, the axis of the planispiral coil varies slightly during growth and the initial stage in these forms is asymmetric (e.g. Fig. 2o, p). This feature is indicative of slight instability in the planispiral mode of coiling and is not suitable for taxonomic discrimination.

Up to six chambers form the uniserial stage. The final chambers in the series are cylindrical with variable inflation of the sides and terminal face. The initial one or two chambers of the series are compressed similar to those in the planispiral coil. The uniserial stage shows little difference in width along its length. The sutures between the final chambers are usually depressed. There is a gradual increase in chamber size during growth, to a maximum test length of 0.66 mm (at stage with six uniserial chambers), but adult chambers are usually broader than high.

The aperture is terminal in the uniserial stage. In final cylindrical chambers it is circular (Fig. 2e), but in the first chamber of the uniseries it may be oblong (Fig. 2d). The apertural outline is variably irregular due to protruding agglutinated grains.

The wall is pale grey when dry, but under water is pale brown with a darker brown outline between chambers in the initial coil. The agglutinated grains are poorly sorted with a maximum dimension of up to 0.11 mm. Because no other agglutinated types are present, the relative grain size and any indication of selectivity in grain size cannot be assessed. Although most grains are quartz, mafic minerals are conspicuous. Rarely, the siliceous skeletons of ribbon-shaped diatom colonies are incorporated in the wall. However, no carbonate skeletal material is present despite an abundance of carbonate skeletal fragments in the sand fraction of the sediment, nor is there any carbonate cement (the tests do not react when immersed in 5% hydrochloric acid). When immersed in sodium hypochlorite, the brown matrix within the test is bleached and the walls disaggregate thereby indicating an organic cement.

2. Kalgan River

All specimens in the Kalgan River assemblage (Fig. 3) belong to global morphotype A; however, they have a less regular outline than those from the Wellstead Estuary because the average grain size of the agglutinated material in the test is coarser. The maximum size of grains observed in the test is 0.17 mm compared to 0.11 mm in the Wellstead Estuary assemblage (Table 4). As in the former, the test contains no carbonate component, and the cement is organic. In comparison to the other agglutinated species present in the sample, the test is much more coarsely agglutinated and the surface is rougher than in the fine-grained, slightly rough *Scherochorella* and *Caronia* and the very fine-grained and smooth *Trochammina* and *Haplophragmoides*. The *Ammobaculites* may be agglutinating the coarsest quartz and mafic grains available to them in the sediment. Confirmation of this requires a sediment grain-size analysis. No biogenic carbonate fragments are included in the test.

The diameter of the planispiral coil has a larger range than for the equivalent initial stage in specimens from Wellstead Estuary, but a similar number of chambers in the final whorl is present (viz. 6–7). Because of the coarse agglutination, in many specimens the umbilicus is not a well-defined hollow and sutures between chambers are obscure. Irregularities in initial coiling are present similar to those observed in some of the Wellstead Estuary specimens. The uniserial chambers are defined by depressed sutures, at least between the final chambers. The maximum number of uniserial chambers found is four (Table 4; Fig. 3) and the uniserial chambers increase gradually in size with little change in width through the series. Adult uniserial chambers are cylindrical (Fig. 3d, f), whereas the early uniserial chambers tend to be slightly compressed (Fig. 3e). In most specimens the shape of the terminal aperture is variable due to the coarse-grained test, but is more elongate in early uniserial chambers (Fig. 3d, e).

Some tests with the largest diameters of the planispiral coil (0.33 – 0.36 mm; Fig. 3a, f, h), limited uniserial development, and maximum test lengths of 0.43 – 0.47 mm are either extreme variants within the morphotype

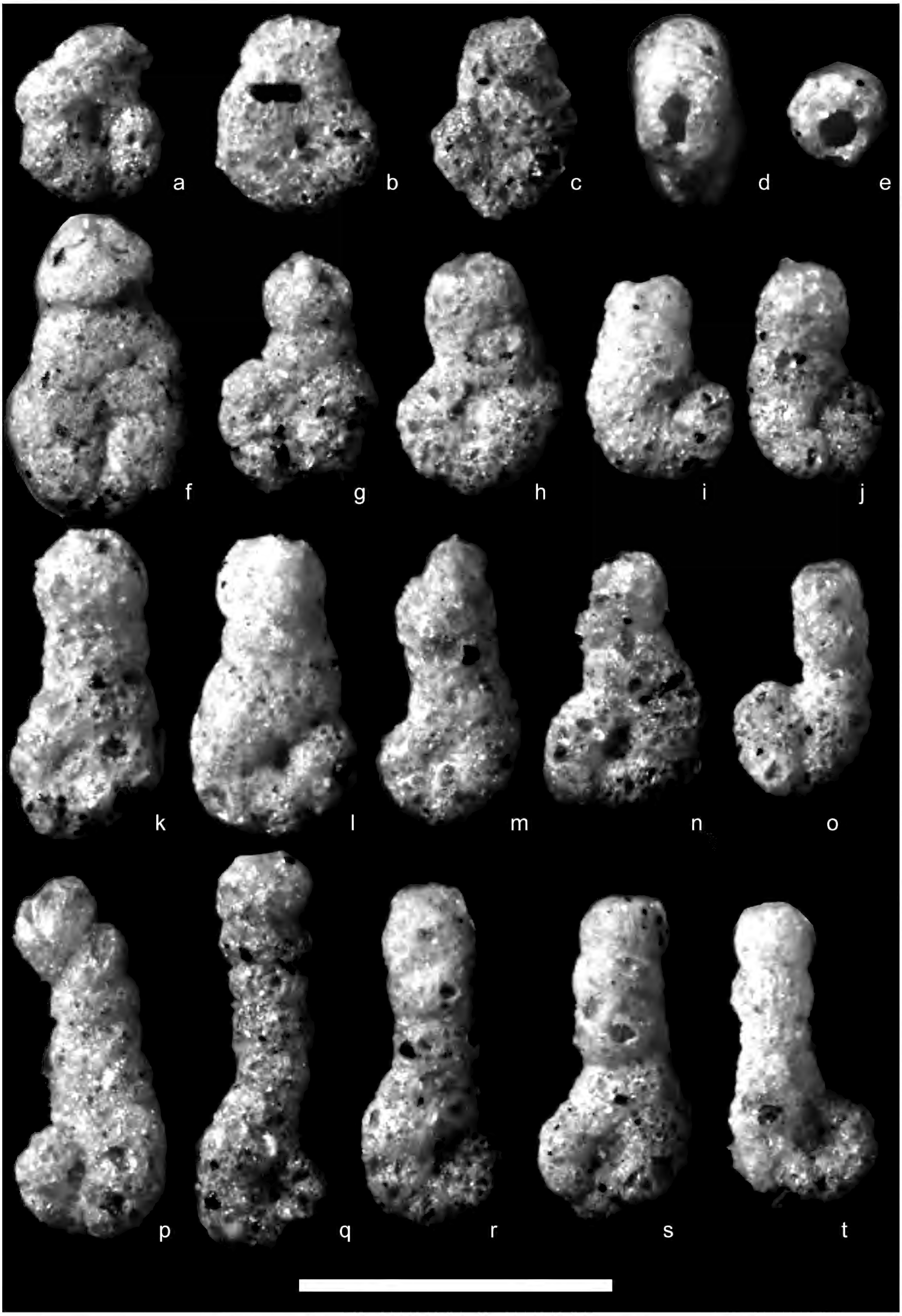

Figure 2. *Ammobaculites* assemblage from Wellstead Estuary, locality 1. All specimens belong to global estuarine morphotype A, and are assigned to *Ammobaculites* sp. ex. gr. *A. exiguus* (Cushman & Bronnimann); d and e are apertural views. Bar scale is 0.5 mm.

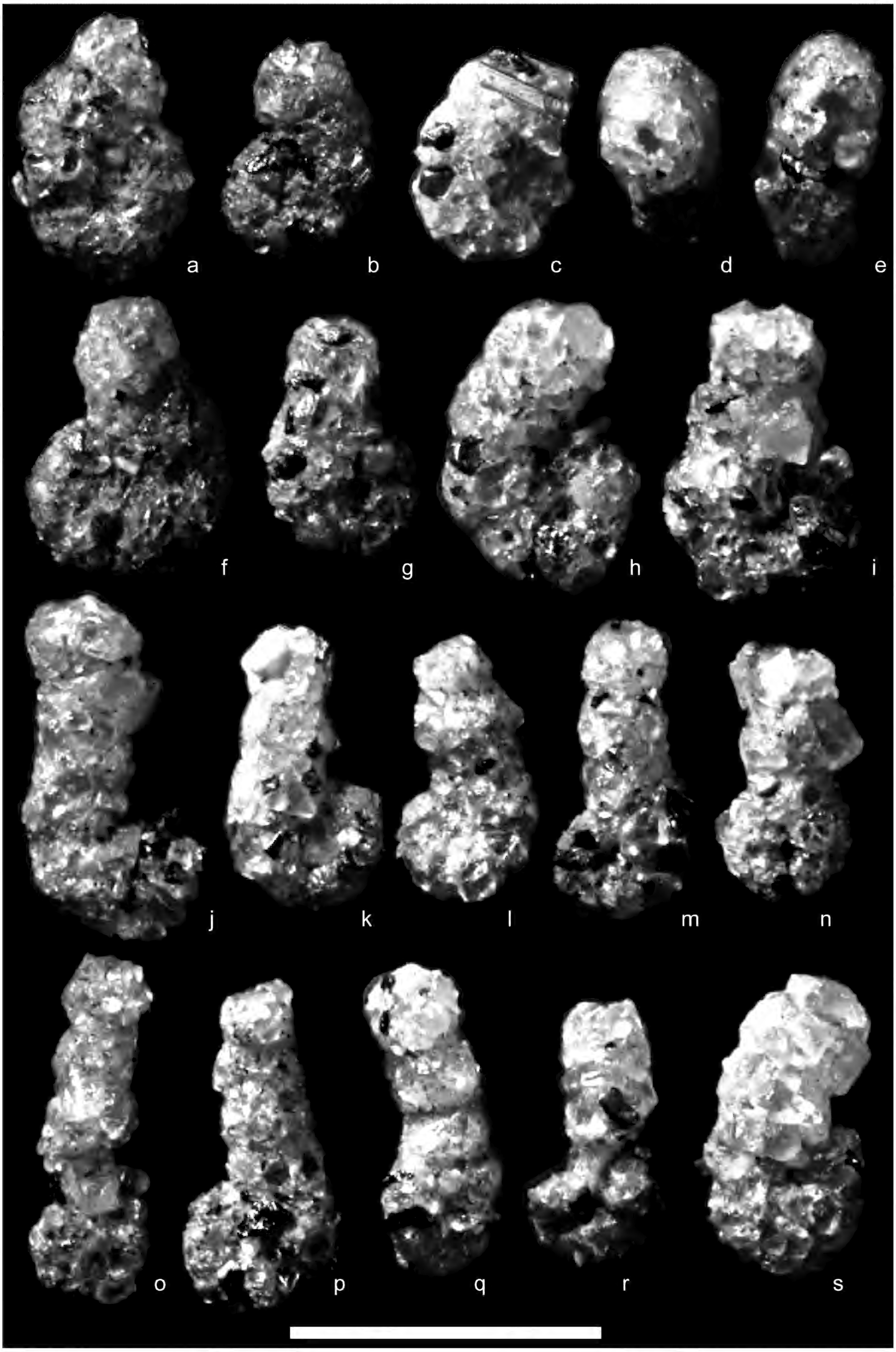

Figure 3. *Ammobaculites* assemblage from Kalgan River, locality 2. All specimens belong to global estuarine morphotype A, and are assigned to *Ammobaculites* sp. ex. gr. *A. exiguus* (Cushman & Bronnimann); d and e are apertural views. Bar scale is 0.5 mm.

A complex or belong within morphotype E (Table 1; see later discussion). They could also be dimorphs in the reproductive cycle. A much larger sample size and molecular analyses of living specimens is required in order to resolve this question.

3. Frankland River

The limited assemblage of *Ammobaculites* found here is included in this discussion because the only tests that have comparable planispiral stages to those at sites 1 and 2, lack well developed uniserial stages (Fig. 4a–i). The maximum diameter of the planispiral coil, the number of chambers in the last whorl, and the non-carbonate composition and coarsely agglutinated rough surface of the wall are similar to those found at the previous sites. Among the other agglutinated foraminifers at this locality, *Miliammina* has a slightly rough, fine-grained wall; and *Trochammina* and *Haplophragmoides* have very fine-grained smooth walls.

At this locality tests have only developed to an early uniserial stage. Possibly suitable environmental conditions for their development are short because the large seasonal influx of freshwater through the river keeps salinity very low for long periods (see Appendix 1). This can be tested through examining the development of living specimens from this site in laboratory cultures at optimum conditions.

Rare specimens of a robust morphotype (Fig. 4j) that appears to be a different *Ammobaculites* are present at this site. The coarsely agglutinated wall obscures the chamber arrangement, but an initial tight coil (perhaps with an irregular coiling axis) is followed by a uniseries of three broad cylindrical chambers. The aperture is terminal and rounded. Further material is required before the generic identification can be confirmed. Similar forms are present in the Walpole Inlet and Hardy Inlet assemblages.

4. Walpole Inlet

The assemblage in Walpole Inlet includes two distinct morphotype groups: A (Fig. 5a–i, k, ?j) and B (Fig. 5m–u). Morphotype A consists mainly of tests that include only the planispiral stage and rarely the addition of a single uniserial chamber. These are slightly smaller in diameter than equivalent growth stages at sites 1–3 and 5 (Table 4). They are morphologically similar to the common types found in the Frankland River at site 3 and have similar wall characteristics. Rare specimens (e.g. Fig. 5g, h) have a more developed uniserial stage of up to four chambers. The adult uniserial stage is cylindrical and the aperture is terminal (Fig. 5f, h).

The other group (B) represented here belongs with the robust specimen (Fig. 4j) from the Frankland River. These tests are more coarsely agglutinated than morphotype-A specimens and reach a longer test length at a growth stage with four uniserial chambers. The uniserial stage is erect above the initial coil. Because of the coarse agglutination, the chamber arrangement is variably obscure, especially in the initial coil, which has about four bulbous chambers exposed. Initial coiling in many of the specimens seems slightly irregular, but not

Table 4

Measurements made on the illustrated assemblages of *Ammobaculites* in the south coast estuaries. Diameters of the initial coil and the width and length of uniserial stage and test are given as an average with the range of values in parenthesis. All dimension measurements are in millimetres.

Character	1. Wellstead Estuary	2. Kagan River	3. Frankland River	4. Walpole Inlet	5. Hardy Inlet
Max. diameter initial coil	0.25 (0.21–0.30)	0.27 (0.19–0.36)	0.26 (0.19–0.30)	A. 0.23 (0.18–0.27) B. 0.19 (0.16–0.22)	A. 0.26 (0.22–0.30) B. 0.23 (0.20–0.29)
No. chambers in final whorl of coil	5–7	~ 6	~ 6	A. ~ 6 B. ~ 4	A. ~ 6 B. ~ 4
No. uniserial chambers	1–6	1–4	0–1	A. 0–4 B. 1–4	0–4
Max. width 1st uniserial chamber	0.16 (0.12–0.22)	0.16 (0.13–0.24)	0.15 (0.11–0.18)	A. 0.12 (0.09–0.16) B. 0.14 (0.12–0.16)	A. 0.15 (0.12–0.17) B. 0.19 (0.15–0.22)
Max. width last uniserial chamber	0.15 (0.12–0.19)	0.16 (0.11–0.19)		A. 0.14 (0.12–0.14) B. 0.17 (0.14–0.20)	A. 0.14 (0.12–0.16) B. 0.20 (0.12–0.27)
Max. width uniserial stage	0.16 (0.12–0.22)	0.17 (0.15–0.24)		A. 0.14 (0.11–0.14) B. 0.17 (0.14–0.20)	A. 0.15 (0.12–0.16) B. 0.21 (0.15–0.27)
Max. length uniserial stage	0.25 (0.11–0.44)	0.25 (0.11–0.39)	0.10 (0.08–0.13)	A. 0.16 (0.07–0.25) B. 0.21 (0.09–0.38)	A. 0.18 (0.12–0.26) B. 0.35 (0.25–0.56)
Max. length test	0.45 (0.28–0.66)	0.47 (0.36–0.56)	0.31 (0.24–0.38)	A. 0.34 (0.26–0.50) B. 0.36 (0.25–0.52)	A. 0.37 (0.28–0.44) B. 0.53 (0.39–0.77)
Max. grain size in wall	0.11	0.17	0.11	A. 0.10 B. 0.13	A. 0.14 B. 0.12
No. specimens measured	18	16	9 (5 with uniserial stage)	A. 9 (7 with uniserial stage) B. 7	A. 10 (9 with uniserial stage) B. 5

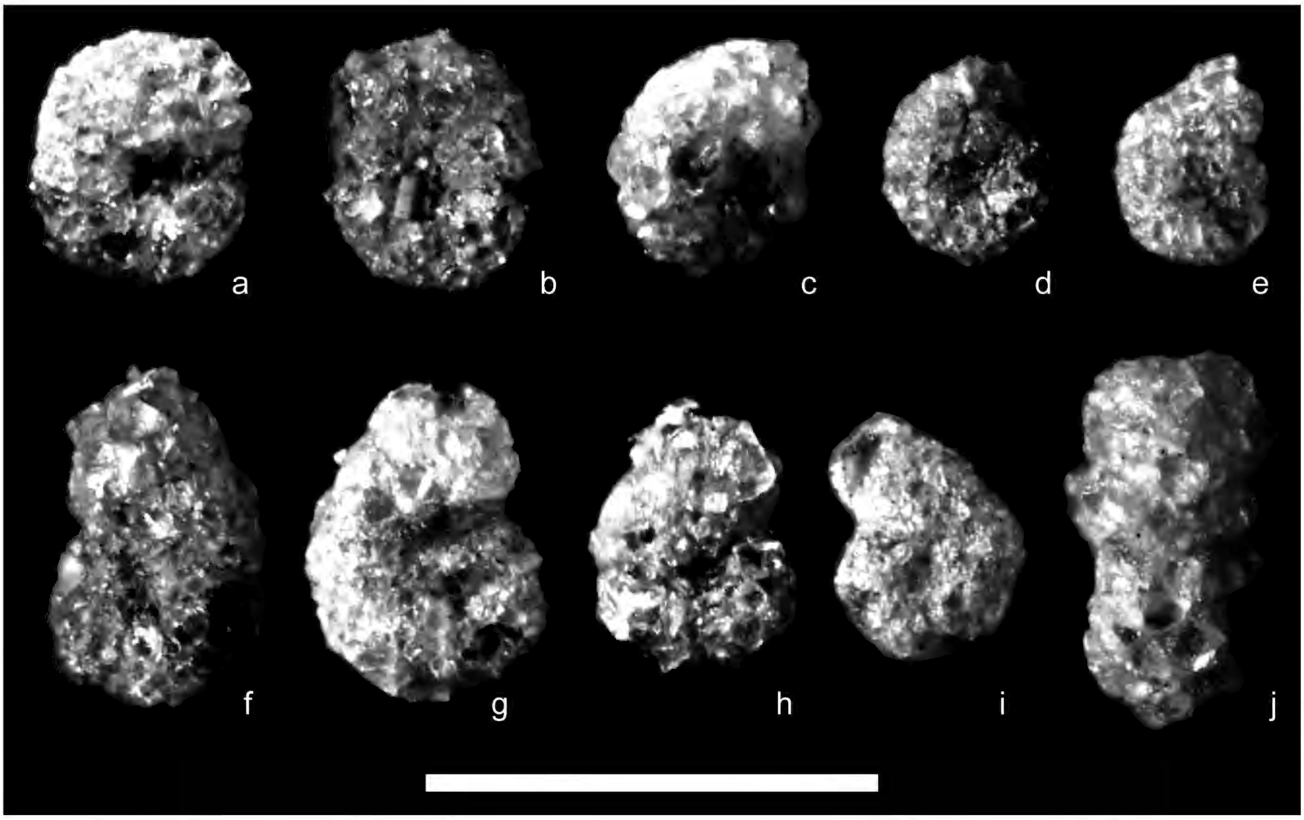

Figure 4. *Ammobaculites* assemblage from Frankland River, locality 3. Specimens a–i are considered to be juveniles of global estuarine morphotype A and are assigned to *Ammobaculites* sp. ex. gr. *A. exiguus* (Cushman & Bronnimann). Specimen j is a representative of global estuarine morphotype B and is left in open nomenclature as *Ammobaculites* sp. Bar scale is 0.5 mm.

streptospiral as in *Bulbobaculites* Maync. The aperture is a similar terminal opening (Fig. 5u) but is often blocked by agglutinated or extraneous material (Fig. 5p). Many live foraminifers when disturbed agglutinate grains over apertures and any other large pores (e.g. Haig *et al*. 2020, fig. 14G).

Both morphotypes have non-carbonate, organic-cemented walls. They have incorporated grains of a larger size in their tests compared to the accompanying more finely agglutinated genera with rough walls (*Caronia* and *Miliammina*).

5. Hardy Inlet

The two morphotype groups (A and B) found in Walpole Inlet and the Frankland River are also present at site 5 in the Hardy Inlet. The majority of specimens in morphotype A (Fig. 6a–j, q, r) show a greater development of the uniserial stage and are more coarsely agglutinated than those from Walpole Inlet (Table 4). They resemble more closely the Kalgan River specimens.

Morphotype B is represented by few specimens (Fig. 6k–p), but these are more robust and have the four bulbous chambers exposed in the initial coil followed by up to four uniserial chambers as at Walpole Inlet.

The morphotypes here are much more coarsely agglutinated than the accompanying agglutinated foraminifers. The coarsely agglutinated rough wall contrasts with the finely agglutinated rough wall of accompanying *Miliammina* and *Scherochorella*, and the very fine smooth wall of *Trochammina*.

Summary of morphotypes

Two morphotype groups, following those outlined in Table 1, are represented in the studied estuarine samples. Morphotype A is present at each site and is characterized by an initial involute coil with 6–7 chambers in the final whorl followed by a uniserial stage, excentric above the coil, of up to four chambers, rarely as many as six in a maximum test length of 0.66 mm. The adult uniserial stage is cylindrical with little variation in width but is narrower than the initial coil. The wall is coarsely agglutinated and roughly finished. Juvenile tests with only the planispiral stage are present at each locality and at one site (Frankland River) they are the only forms found. In the Kalgan River assemblage, individuals with a broader than usual initial coil and a reduced uniserial stage may represent morphotype E or be at the extreme edge of the variability range of group A.

Less common representatives of morphotype B are present in the three western estuaries: Frankland River, Walpole Inlet and Hardy Inlet. These are more robust than the group A types, more coarsely agglutinated and reach a larger test length (0.77 mm at the fourth chamber of the uniserial stage). Although the initial coil seems to have a consistent four bulbous chambers exposed, the coil in some specimens is irregular. The cylindrical uniserial stage is positioned centrally above the coil.

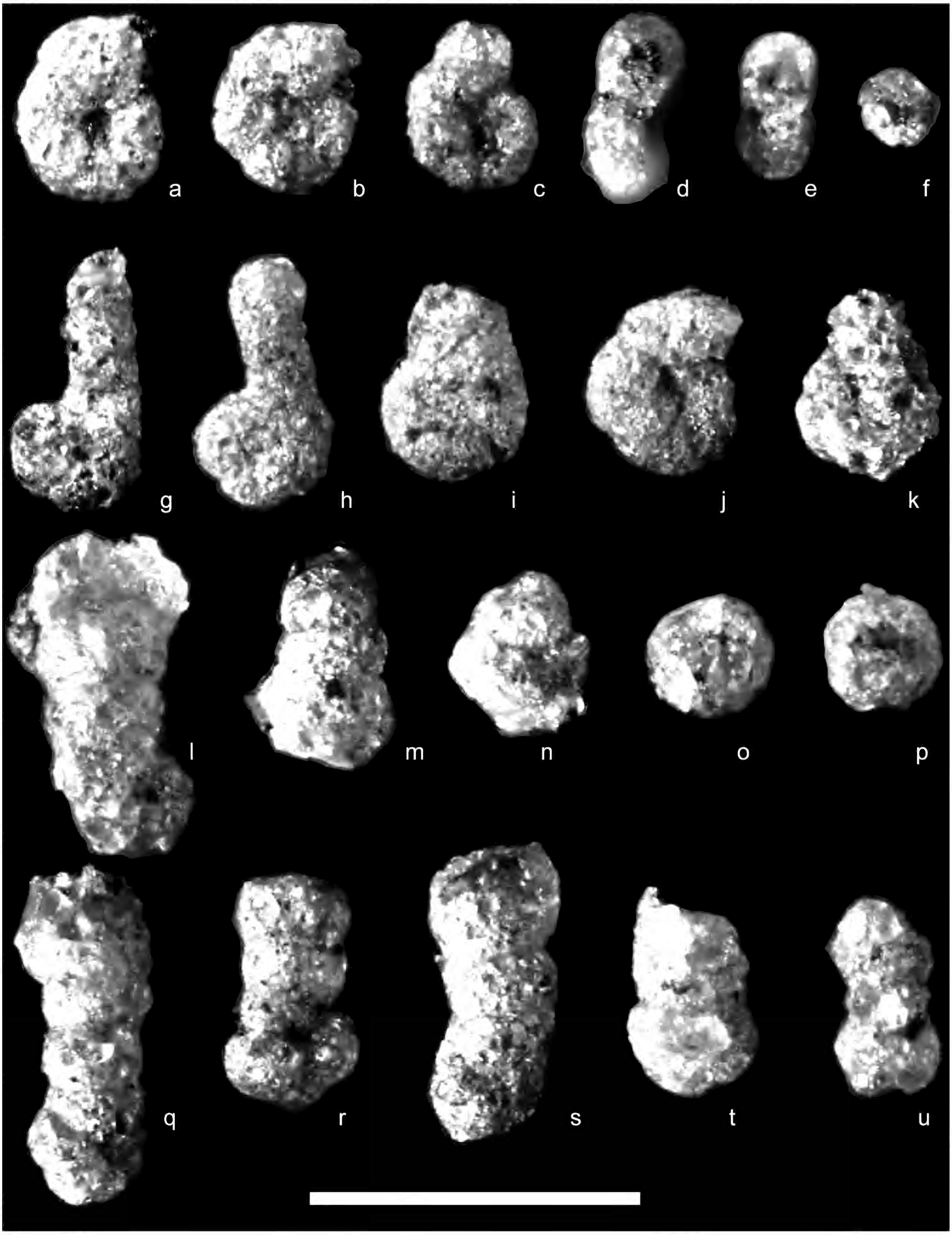

Figure 5. *Ammobaculites* assemblage from Walpole Inlet, locality 4. Specimens a–k belong to global estuarine morphotype A and are assigned to *Ammobaculites* sp. ex. gr. *A. exiguus* (Cushman & Bronnimann). Specimens l–u belong to global estuarine morphotype B and are left in open nomenclature as *Ammobaculites* sp. Bar scale is 0.5 mm.

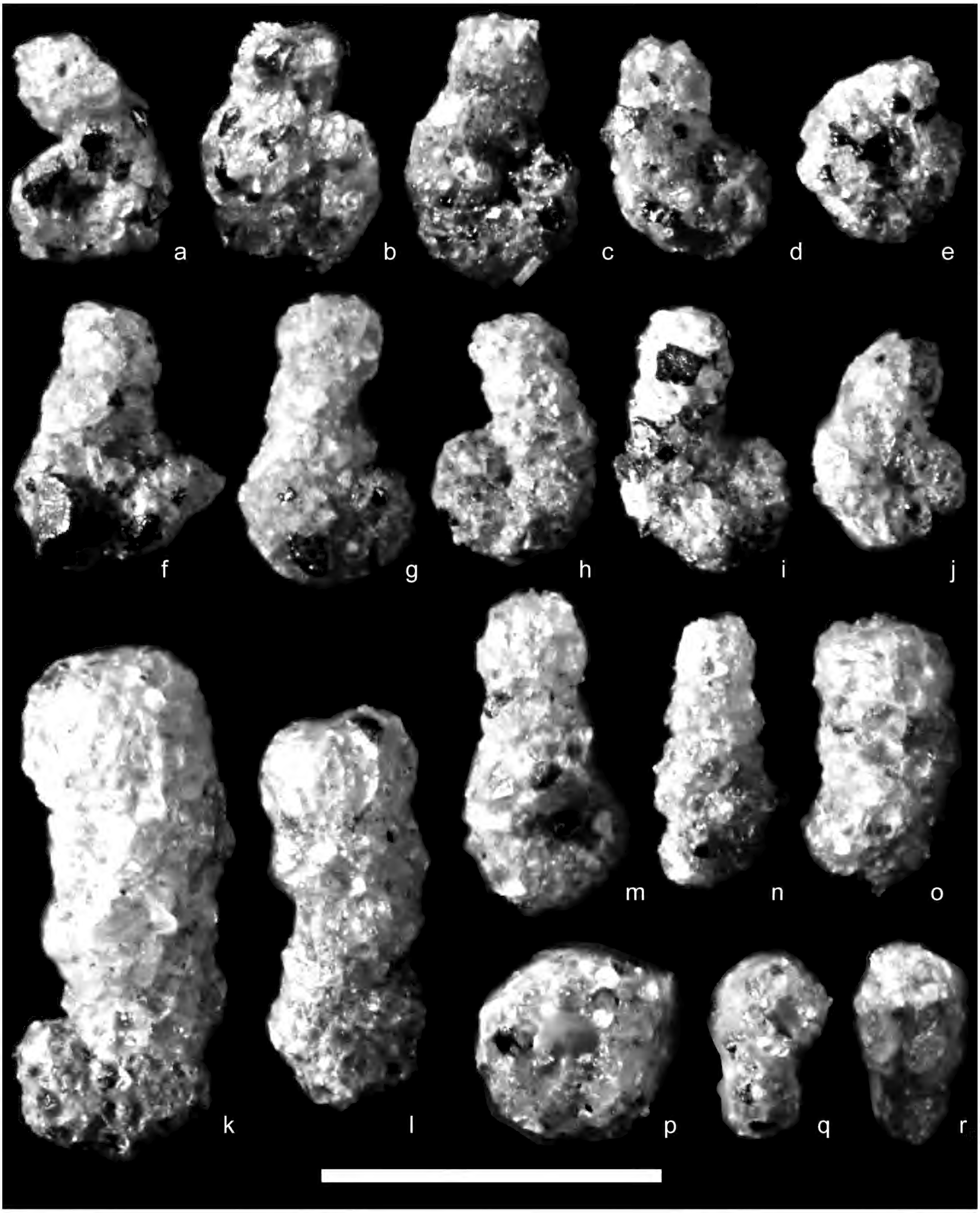

Figure 6. *Ammobaculites* assemblage from Hardy Inlet, locality 5. Specimens a–j, q, and r belong to global estuarine morphotype A and are assigned to *Ammobaculites* sp. ex. gr. *A. exiguus* (Cushman & Bronnimann); q and r are apertural views. Specimens k–o, and p belong to global estuarine morphotype B and are left in open nomenclature as *Ammobaculites* sp.; p is an apertural view. Bar scale is 0.5 mm.

Agglutinated quartz is the main component of the wall in both morphotypes, but conspicuous mafic grains are also present. Grain-size selectivity is obvious compared to the accompanying agglutinated foraminifers of other genera. The tests do not contain carbonate material, although an abundance of carbonate skeletal debris is present within the mud at some of the sites. An organic cement binds the grains.

Based on morphological criteria, each group probably represents just one species. Molecular (rDNA) gene sequence analyses are required in order to determine the genetic diversity here. Several factors make such a study of particular interest: (1) the studied river systems are separated by large distances and are not interconnected at present nor in the past; (2) the estuaries are closed to the open ocean for long intervals or have tenuous connections to the ocean; (3) the mud habitats of the *Ammobaculites* assemblages are confined to parts of the estuaries and are not contiguous through the estuaries and onto the high-energy inner continental shelf which has a well-sorted sand substrate. These *Ammobaculites* populations may have remained isolated for a considerable time with the only connection between them coming from chance migration, for example in mud on birds' feet.

COMPARISON TO KNOWN AUSTRALIAN *AMMOBACULITES*

Most previous records of *Ammobaculites* in modern Western Australian estuaries belong to morphotype A but have been attributed to three different species named from outside the Australian region with a further two left in open nomenclature (Table 3). An additional species, tentatively assigned to *Ammobaculites* (viz. *A. yardiensis* Parker 2009), is certainly distinct but requires further study, particularly of the initial chamber arrangement.

Previous reports of morphotype A in Western Australia include the illustrated specimens of McKenzie (1962), Quilty (1977) and Quilty & Hosie (2006) referred to *A. agglutinans*, *A. exiguus* of Ostrognay & Haig (2012), and *A. villosus* and perhaps *A.* sp and *Haplophragmoides* sp. (as juvenile morphotypes) as recognized by Revets (2000). All of these forms seem to lie within the morphological range exhibited by morphotype A in the estuaries studied here and possibly belong to the one species.

In eastern Australia (Table 3), of specimens assigned to *A. exiguus* and *A. agglutinans*, only those illustrated by Strotz (2012, 2015) from central New South Wales estuaries closely resemble the Western Australian morphotype A. These have about six chambers in the initial broad coil and a rough coarsely agglutinated wall. The specimen from South Australia illustrated by Cann *et al*. (2000) and attributed to *A. barwonensis* may be equivalent (see discussion below), as well as the morphotype identified by Yassini & Jones (1995) as *A. subcatenulatus* (it lacks the evolute initial coil and the elongate uniserial chambers of the holotype of *A. subcatenulatus*, here referred to morphotype D, Table 1).

Ammobaculites sp. of Quilty (1977, fig. 11) from Hardy Inlet belongs to morphotype B that is also reported in the present study from this inlet and from the Frankland River and Walpole Inlet. The elongate specimen identified as *Psammosphaera* sp. by Quilty (1977, p. 87, fig. 7), with an especially atypical test shape for this genus, may also belong here. This morphotype has not been illustrated from eastern Australian assemblages.

The eastern Australian form referred to *Ammobaculites barwonensis* by Apthorpe (1980), Bell & Drury (1992), Bell (1995, 1996) and Strotz (2003), and transferred to *Simobaculites* by Strotz (2012, 2015) is distinct from Western Australian *Ammobaculites* and belongs within global morphotype C (Table 1). It seems close to *Ammobaculites amarus* Hada (1957). Whether the type specimen of *Ammobaculites*? *barwonensis* as figured by Collins (1974, pl. 1, figs 3a, b) belongs within the highly variable range of morphotype C at the other localities has not been documented at the type locality where one specimen has been described. Collin's type specimen may equally fit within morphotype A because it has a cylindrical uniserial stage positioned excentrically above a broad initial coil of comparable dimensions to the morphotype-A individuals reported from Western Australia and appears to have, as drawn, a similar rough coarsely agglutinated wall. Morphotype A differs from the eastern Australian morphotype C by having a rougher, usually more coarsely agglutinated wall, consistent cylindrical adult uniserial chambers with circular cross-sections, as well as an absence of flaring of the uniserial stage in the spectrum of variability found in one assemblage.

COMPARISON TO GLOBAL ESTUARINE *AMMOBACULITES*

Among known estuarine species attributed to morphotype A (Table 1) the Western Australian representatives of this group are most similar in outline to *A. exiguus* but are larger relative to growth stage, both in the initial coil and the uniserial stage. This may reflect environmental influence. The holotype and paratype illustrated by Cushman and Bronnimann (1948) demonstrate extremes of variability in the uniserial stage (erect to slightly irregular) that is also illustrated by the Western Australian specimens. The holotype housed in the Smithsonian National Museum of Natural History, and refigured by a rendered reflected-light image (http://n2t.net/ark:/65665/3ff5d8631-13b2-4433-ba2d-90d90d101632) seems morphologically very similar in particular to some of the specimens from Wellstead Estuary (e.g. Fig. 2r, s). *Ammobaculites exiguus* has been recorded from many localities world-wide (Hayward *et al*. 2018).

It seems improbable that a Western Australian estuarine *Ammobaculites* could be conspecific with a Middle Miocene deep open-water species of the genus. The lectotype of *Ammobaculites agglutinans*, as illustrated by SEM image (Papp & Schmid 1985, pl. 45, fig. 7), is much larger than any specimen recovered in Western Australian assemblages. This specimen has fewer chambers in the final whorl of the planispiral coil and has adult uniserial chambers becoming slightly longer than wide at the fourth uniserial-chamber stage (in contrast to the relatively broad, lower chambers of most of the Western Australian specimens). On

morphological grounds, the Western Australian types are not conspecific with the type species of *Ammobaculites* (viz. *A. agglutinans*). None of the other morphotype A species known globally in estuaries (Table 1) closely resemble the specimens studied here.

Revets (2000) placed a group-A individual (see Table 2) in *Ammobaculites villosus*. Saidova's (1975) species is here attributed to morphotype B with erect uniserial stage centrally placed above the initial coil (Table 1). This is a much larger upper bathyal species, with type locality at 156 m off the west coast off the South Island of New Zealand, than the estuarine Western Australian type. Specimens from the Timor Sea assigned to *A. villosus* by Loeblich and Tappan (1994, pl. 7, figs 12–15) are group-A morphotypes that more closely resemble the lectotype of *A. agglutinans* than Saidova's (1975) type illustration of *A. villosus*.

Among *Ammobaculites* of group B in the global estuarine fauna (Table 1), the holotype and paratypes of *Ammobaculites balkwilli* have about four inflated chambers exposed in the initial coil similar to the specimens of this group found in the studied Western Australian estuaries. However, the shape of adult uniserial chambers (elongate in *A. balkwilli*) differs from the Western Australian types which have lower uniserial chambers. The specimen figured as *A. balkwilli* by Allen *et al*. (1999, pl. 1, fig. 4) seems closer to *A. exiguus* (morphotype A) than to typical *A. balkwilli* (morphotype B). *Ammobaculites josephi,* another coastal group-B species (Table 1), also has more elongate adult chambers than the Western Australian form.

COMPARISON TO AUSTRALIAN FOSSIL *AMMOBACULITES*

Among the Australian fossil assemblages are representatives of morphotypes A, B, C and E (Fig. 7). Most of the fossils, which range from Permian to Cretaceous, were recovered from friable mudstone by physical disaggregation and washing the sample using water over a 150 µm-mesh sieve. Within these agglutinated assemblages, tests contain no carbonate material although accompanying foraminifers usually include types with calcite/aragonite walls with crystalline ultrastructure. As noted by Haig (1980, 2003, 2004, 2018) and Haig & McCartain (2010), the fossil *Ammobaculites* from the shale facies often have distorted deflated tests deformed during burial in sediment and indicative of an original flexible shell due to organic cement binding the grains as in the modern types. During early diagenesis in the sediment, siliceous cement as overgrowths on agglutinated grains bind the test into a rigid fossil. When recovered by HCl acid digestion from early diagenetic calcareous mudstone nodules which are present at some horizons within the mudstone successions, perfectly preserved tests emerge in the residue (e.g. Haig & Barnbaum 1978, fig. 2g) but these often fall apart due to lack of cement when touched by a fine brush.

Ammobaculites belonging to morphotypes A and B from very shallow-water mud facies in the Australian Permian (e.g. Fig. 7a–h) and Cretaceous (e.g. Fig. 7x–zg) have rough, coarsely agglutinated walls similar to the modern estuarine types in Western Australia, and agglutinate some of the largest grains available in their life environment compared to some of the accompanying agglutinated species. This may be a very conservative genetic character for these morphotype groups within the genus. The Triassic types (e.g. Fig. 7i–s) come from deeper-water more open-marine calcareous mud facies where coarse grains in the sand fraction of the sediment are lacking.

As noted by Haig & McCartain (2010), significant diversification among *Ammobaculites*-related groups commenced during the Triassic, with *Kutsevella* Dain (1978), resembling modern morphotype E, firmly established by this time (e.g. Fig. 7t–v). Elsewhere, *Kutsevella* is well known from the Jurassic, and is common in shallow-water mud facies of the Australian mid-Cretaceous interior sea (Fig. 7zk, zl). These types correspond to morphotype E among modern assemblages (Table 1), and are morphologically similar to the large planispiral forms found in the Kalgan River (e.g. Fig. 3a, f, h).

Among *Ammobaculites*-related groups, the Australian mid-Cretaceous assemblages show further diversification although this commenced during the Jurassic elsewhere. *Bykoviella* Korchagin (1964) with slightly irregular broad initial coil and reduced uniserial stage (e.g. Fig. 7zh) and *Simobaculites* Loeblich & Tappan (1984) with broad initial coil and moderately compressed uniserial stage are present in the restricted-marine mud facies of the Australian Cretaceous. It is remarkable how similar *Simobaculites raghavapuramensis* (e.g. Fig. 7zi, zj) described by Taylor & Haig (2001) from the Barremian Muderong Shale of the Southern Carnarvon Basin is to the modern morphotype C types from eastern Australia attributed to *Simobaculites* by Strotz (2012, 2015). Not only is the architecture of the test similar but the finely agglutinated smooth wall is also equivalent. The modern and Cretaceous types co-occur with coarsely agglutinated rough-surfaced morphotype A representatives.

Another addition in the Australian Cretaceous is the appearance of rare *Ammomarginulina* Wiesner (1931) in the interior-sea mud facies (e.g. Fig. 7zm). These seem to be among the oldest *Ammomarginulina* known in the global record. Species of the genus differ from those of *Ammobaculites* in the inclined chambers (and sutures) of the uniserial stage. *Ammomarginulina* is absent from Western Australian estuarine assemblages, but is known from such faunas elsewhere (sometimes designated as *Ammobaculites* or *Ammotium* Loeblich & Tappan 1953 which typically has an *Astacolus*-like rather than *Marginulina*-like adult chamber arrangement).

DISCUSSION

This reconnaissance analysis of *Ammobaculites* from estuaries along the south coast of Western Australia, raises three major questions:

1. For organisms that live in isolated benthic mud habitats in unconnected estuaries, why do similar morphotypes appear in these environments? Are they the same species? If so, what are the means of species dispersal in what are marginal-marine, ephemeral, unconnected habitats.

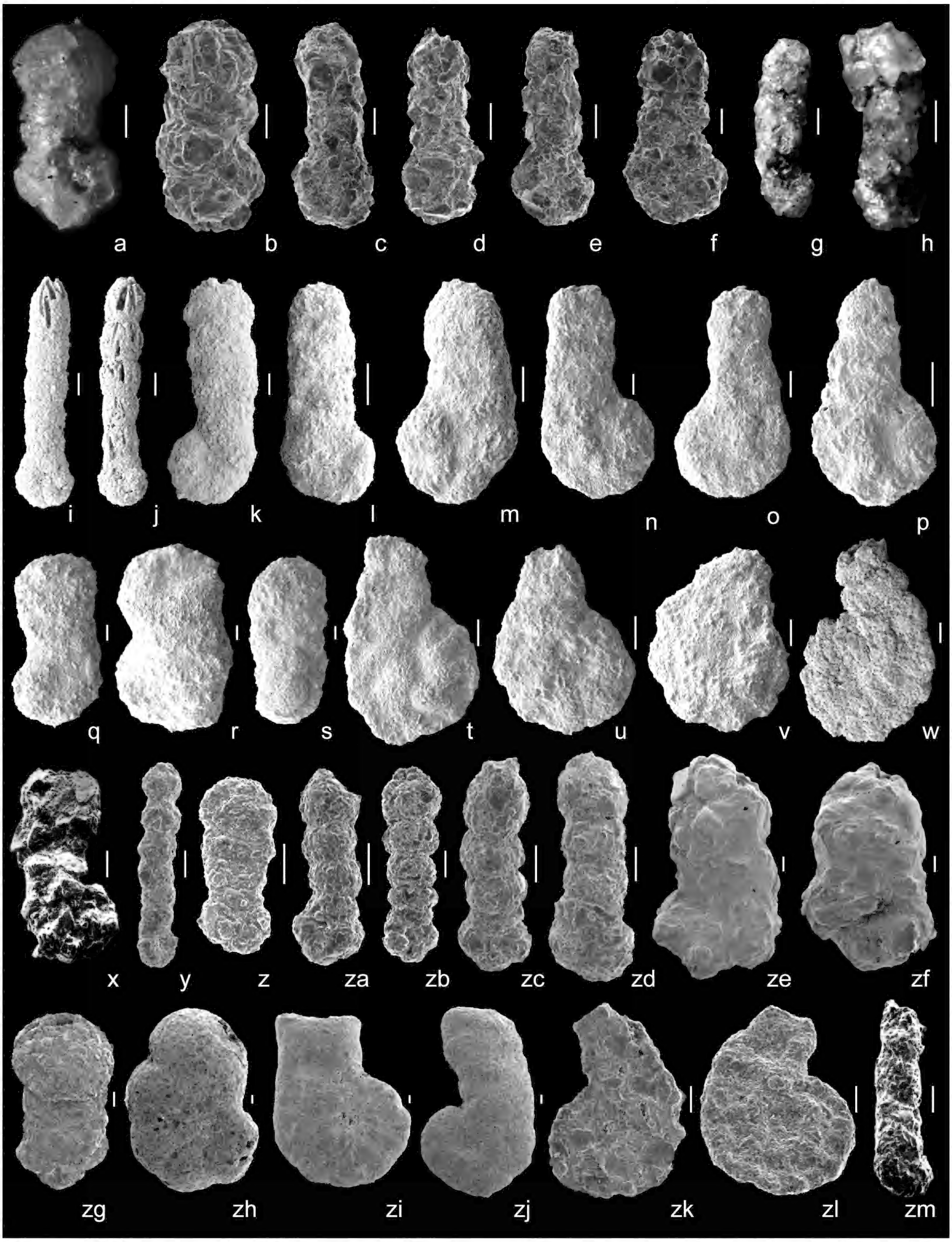

Figure 7. Fossil *Ammobaculites* from mud facies of Eastern Gondwanan-Australian interior seas. Bar scales are 0.1 mm. Specimens a–h, Permian species; a, *Ammobaculites* sp. belonging to morphotype B, from Haig (2018); b–f, *Ammobaculites woolnoughi* belonging to morphotype A, but transitional to B, from Haig (2003); g, h, *Ammobaculites wandageensis* belonging to morphotype A, from Haig & Mory (2016). Specimens i–w, Triassic species; i, j, *Ammobaculites duncani* belonging to morphotype B, from Haig & McCartain (2010); k–o, *Ammobaculites rhaeticus* belonging to morphotype A, from Haig & McCartain (2010); p, t–v, *Kutsevella beggi* belonging to morphotype E, from Haig & McCartain (2010); q–s, *Ammobaculites zlambachensis* belonging to morphotype A, from Haig & McCartain (2010); w, *Carteriella manelobasensis*, although with broad planispiral coil and uniserial adult stage, may not be closely related to *Ammobaculites* but a derivative of *Haplophragmoides*–*Labrospira*, from Haig & McCartain (2010). Specimens x–zm, Cretaceous species; x, *Ammobaculites australis* belonging to morphotype A, from Haig (1980); y, *Ammobaculites humei* belonging to morphotype B, from Campbell & Haig (1999); z–zd, *Ammobaculites humei* belonging to morphotype B, from Dixon *et al*. (2003) and Haig *et al*. (2004); ze, zf, *Ammobaculites grossus* belonging to morphotype B, from Taylor & Haig (2001); zg, *Ammobaculites hofkeri* belonging to morphotype B, from Taylor & Haig (2001); zh, *Bykoviella* sp. cf. *B. elenae* from Taylor & Haig (2001); zi, zj, *Simobaculites raghavapuramensis* belonging to morphotype C, from Taylor & Haig (2001); zk, zl, *Kutsevella implanus* belonging to morphotype E, from Campbell & Haig (1999); zm, *Ammomarginulina* sp. A of Haig (1980).

2. Why is there such a close similarity between modern *Ammobaculites* species in the estuarine (hyposaline) mud habitats in Western Australia with those in similar situations on remote continents? Is this because of morphological adaption to a similar life habitat or is there a close genetic link as suggested, for example, by the pattern of grain-size agglutination compared with accompanying agglutinated species belonging to other genera.

3. Does the conservatism in morphological evolution witnessed in the fossil record over hundreds of millions of years suggest conservatism in genetic makeup that may also link to the widespread discontinuous distribution patterns of modern assemblages. The distributions of morphological-based species in the fossil record back as far as the Permian, show similar widespread distribution patterns to the modern, essentially cosmopolitan, morpho-species. Intriguing, during the Permian and early Mesozoic, there were no birds' feet to transport mud and the contained living foraminifers from adjacent estuaries or interior seas.

The answers to these questions rely on future detailed biological analyses, especially of molecular rDNA sequences as is being done for another widespread estuarine group centred on the calcareous *Ammonia tepida* (see Holzmann & Pawlowski 2000). Challenges will include identification of living individuals and extraction of uncontaminated protoplasm from the test. Because of its extremely long and seemingly conservative fossil record as one of the earliest multichambered foraminifers, *Ammobaculites* will provide an intriguing subject for this type of research.

In compiling lists of species names for fossil and extant foraminifers, a pragmatic approach is often employed. The present study has shown when morphological variation of the test is investigated, questions about species placements abound. At the reconnaissance stage of this study, a broad morphotype classification is used. The morphotype A individuals from the studied estuaries seem to belong to one species, but this needs testing by molecular methods. They are designated as "*Ammobaculites* ex. gr. *A. exiguus*" because of morphological resemblance to *Ammobaculites exiguus*. The morphotype-B species has no close estuarine counterpart known elsewhere and is left in open nomenclature (viz. *Ammobaculites* sp.)

CONCLUSIONS

1. Assemblages of *Ammobaculites* from five localities in estuaries on the south coast of Western Australia are described. The assemblages come from mud facies in hyposaline parts of the estuarine systems, including Wellstead Estuary, Kalgan River, Frankland River, Walpole Inlet and Hardy Inlet.

2. Five main morphotype groups (designated A–E) recognized among the global estuarine fauna are used for comparison with the morphotypes at the studied sites. The Western Australian types belong to two widespread groups known elsewhere: (A) species with an initial broad involute planispiral coil and a later cylindrical uniserial stage of lesser diameter positioned excentrically above the coil; and more rarely (B) species with a cylindrical uniserial portion positioned centrally above the initial involute planispiral coil. Rare large specimens from the Kalgan River approach morphotype E (viz. species with broad planispiral coil, and only slight development of a compressed excentric uniserial stage) but may be extreme variants of morphotype A at this locality. Morphotype D (like A, but with a partially evolute initial coil) has not been located. Despite being known from eastern Australian estuaries morphotype C (viz. species with broad initial involute coil and excentric variably compressed and slightly to distinctly flabelliform uniserial stage, with elongate terminal aperture) is absent from the known Western Australian assemblages.

3. The Australian fossil record of *Ammobaculites* in Permian, Triassic and Cretaceous mud facies contains very similar morphotypes to their modern counterparts, and suggest great conservatism in morphological evolution. This also may apply to grain-size selectivity in test construction.

4. The modern *Ammobaculites* are living fossils and future biological research on these organisms, including using molecular techniques, may answer intriguing questions about dispersal from isolated and ephemeral estuarine mud habitats over regional and global scales, and also about the tempo of genetic drift and evolution in this genus. Greater knowledge of habitat and life strategies may provide insights into the palaeoenvironments of ancient larger estuarine-like basins where *Ammobaculites* fossils are common.

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Appendix 1

Localities of studied *Ammobaculites* assemblages, and associated foraminifers.

No.	Locality	Description	Foraminiferal assemblage
1	Wellstead Estuary, Bremer River at 34.38623°S, 119.37593°E; collected 19 February 2020	~20 cm water depth (low water level due to drought and estuary closed off from sea). Black mud ~2 m out from edge of serpulid reef. No salinity measurement at time of collection. Salinity variable (hyposaline to hyposaline) according to Brearley (2005)	*Ammobaculites* assemblage: Fig. 2a–t; associated foraminiferal genera: *Ammonia* (abundant), *Elphidium* (common), *Quinqueloculina* (rare)
2	Kalgan River at 34.93757°E, 117.97474°S; collected 25 September 2019	~10 cm water depth (toward low tide). Muddy fine sand ~2 m from shoreline close to start of bioturbated zone. Salinity, 33 ppt.	*Ammobaculites* assemblage: Fig. 3a–s; associated foraminiferal genera: *Trochammina* (common), *Scherochorella* (rare), *Caronia* (rare), *Haplophragmoides* (rare), *Ammonia* (rare), *Elphidium* (rare), *Quinqueloculina* (rare)
3	Frankland River at 34.99082°S, 116.81575°E; collected 26 September 2019	~1 m water depth. Muddy sand from edge of reeds along shoreline on eastern bank. Salinity, 5 ppt.	*Ammobaculites* assemblage: Fig. 4a–j; associated foraminiferal genera: *Trochammina* (abundant), *Miliammina* (common), *Ammonia* (abundant), Elphidium (common), Haplophragmoides (rare)
4	Walpole Inlet at 34.97792°S, 116.72483°E; collected 26 September 2019	~2 m water depth. Black muddy sand. Salinity, 15 ppt.	*Ammobaculites* assemblage: Fig. 5a–u; associated foraminiferal genera: *Miliammina* (abundant), *Scherochorella* (common), *Caronia* (rare)
5	Hardy Inlet, Blackwood River at 34.29855°S, 115.16844°E; collected 29 September 2019	~1 m water depth. Muddy bioturbated sand with molluscan shell debris and filamentous "algae". No salinity measurement at time of collection.	*Ammobaculites* assemblage: Fig. 6a–r; associated foraminiferal genera: *Scherochorella* (common), *Miliammina* (common), *Trochammina* (very rare), *Ammonia* (rare), *Elphidium* (rare)

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Effect of an isolated bore on birds in the complex arid landscape of Faure Island, Shark Bay, Western Australia

GRAHAM R. FULTON [1, 2]

[1] *Centre for Biodiversity and Conservation Science, University of Queensland, Brisbane, QLD 4072, Australia.*

[2] *Environmental and Conservation Sciences, Murdoch University, South Street, Murdoch, WA 6150, Australia.*

✉ *grahamf2001@yahoo.com.au*

Abstract

Artificial water points in Australian rangelands have had various adverse effects on native biota. In this study, the terrestrial avifauna of an isolated bore on Faure Island, Shark Bay, Western Australia, was evaluated for drinking and geographical abundance patterns. The bore is in a unique environment close to three major biological boundaries: biogeographical, vegetational, and climatic. The island is also of interest because marsupial species extinct on the mainland (e.g. boodie *Bettongia lesueur*) have been re-introduced there. During a four-day survey, 1626 individuals from 20 bird species were observed. Of the species, 80% showed a gradient in relative concentration across the whole island, in the 100 ha around the bore and within the bore's piosphere. Patterns of drinking and attendance at the bore are also reported. Some birds (e.g. Crested Pigeon *Ocyphaps lophotes* and Little Crow *Corvus bennetti*) increased their relative concentration near the watering point while others (e.g. Silvereye *Zosterops lateralis* and Australasian Pipit *Anthus novaeseelandiae*) decreased. The null hypothesis that the bore had no impact on the distribution of birds was rejected.

Keywords: artificial watering point, rangelands, piosphere, faunal concentration gradient, relative analysis

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INTRODUCTION

The impact of artificial watering points along with the spread of pasture grasses has exacerbated the impact of selective grazing by exotic mammals (Landsberg *et al*. 2003). Through these changes, such watering points potentially pose threats to the persistence of endemic biodiversity in Australia, specifically through facilitating changes in the abundance and range of many species of plants, animals and other organisms (Saunders & Curry 1990; Landsberg *et al*. 1997; James *et al*. 1999). Exotic predators, for example the red fox *Vulpes vulpes*, have moved into arid and semi-arid rangelands through the availability of artificial watering points (Burbidge & McKenzie 1989; James *et al*. 1999). Introduced watering points have proliferated in Australian rangelands with most (outside of the driest deserts) substantially less than 10 km apart (Landsberg & Gillieson 1996).

In Australia's rangelands, some species have increased in abundance while others have been introduced, for example, kangaroos *Macropus* spp., cattle, sheep and goats (Bovidae), Buffel Grass *Cenchrus ciliaris*, Crested Pigeon *Ocyphaps lophotes* and Zebra Finch *Taeniopygia guttata* (Landsberg *et al*. 1997; James *et al*. 1999; Barrett *et al*. 2003; Van Dyck & Strahan 2008). Notable declines include the Paradise Parrot *Psephotus pulcherrimus* (a species that has become extinct) and critical weight range marsupials, which are thought to be indirectly affected from grazing competition and directly threatened by foxes and cats *Felis catus* (Shortridge 1909; Burbidge & McKenzie 1989; Jerrard 2008). Birds that feed and nest on the ground have been one of the most adversely affected groups: examples include Australian Bustard *Ardeotis australis*, Plains-wanderer *Pedionomus torquatus,* and Malleefowl *Leipoa ocellata* (Reid & Flemming 1992; Garnett & Crowley 2000; Olsen 2008). Despite the extreme proliferation of artificial watering points, relatively few studies show how they affect birds (Davies 1977a, 1977b; Landsberg *et al*. 1997; James *et al*. 1999; Howes & McAlpine 2008). Only two studies in Australia systematically recorded the bird species, which came to watering points over the course of a day (Davies 1972; Fisher *et al*. 1972). This type of study can identify what species use the artificial watering points and how they use this resource.

The bore on Faure Island in Shark Bay, Western Australia, presented a unique opportunity to investigate a more isolated bore in the absence of foxes and cats, and where the recolonization by native mammals has begun (Algar *et al*. 2010). The bore is of special interest because it is the only artesian bore on the island (June Gronow in Landgate's Geonoma Database). The island is positioned near the convergence of three significant boundaries: biogeographical, vegetational, and climatic (see detailed descriptions below). Thus, the island supports a diverse terrestrial avifauna (Dell & Cherriman 2008). It is situated within the Shark Bay World Heritage Area and surrounded by the Shark Bay Marine Park.

Aims

The watering point was surveyed to identify:

(1) the bird species using the watering point and their relative abundance;

(2) the drinking patterns of each species; and

(3) the geographical patterns of abundance, within the piosphere and at the bore, compared with the 100-ha zone around the bore and the whole island.

STUDY SITE

Physical and biological positioning

Faure Island (pronounced 'Four' according to Fulton 2011), is isolated from the mainland by ~8 km at the closest point, north of Petit Point, and ~14 km east of Francois Peron National Park on Peron Peninsula (Fig. 1). The island is 5148 ha with a perimeter of ~45 km (Abbott & Burbidge 1995; Burbidge & Morris 2002). The island has been a pastoral property since 1876 (June Gronow in Landgate's Geonoma Database) but is now managed as a private nature reserve by the Australian Wildlife Conservancy. The bore site ID is 2000076 and was drilled on 30 June 1928 to 95.7 m at 25°53'20.8458"S, 113°54'39.2688"E (Joanne Gregory, Department of Water, Western Australia, pers. comm. May 2009); however, Google Maps shows its correct location at 25°53'11.1"S 113°54'32.4"E (Fig. 2).

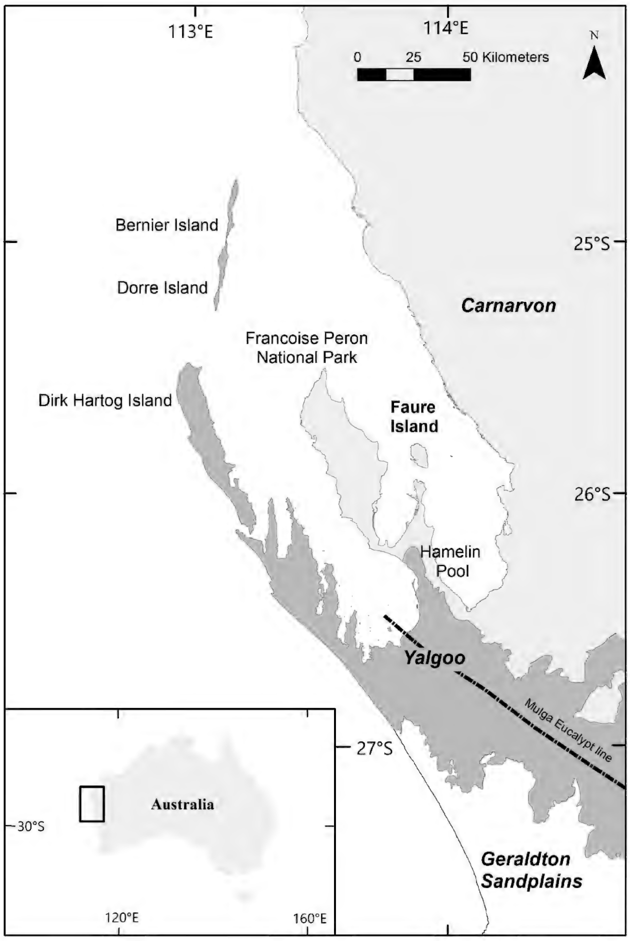

Figure 1. The location of Faure Island, in Shark Bay, in relation to the Mulga/Eucalypt Line approximating Beard (1969; Mulga on the eastern and Eucalypt on the western side). The shaded areas on the map indicate the Geraldton Sandplains, Yalgoo Bioregion and Carnarvon Bioregion (Department of Environment and Energy 2018).

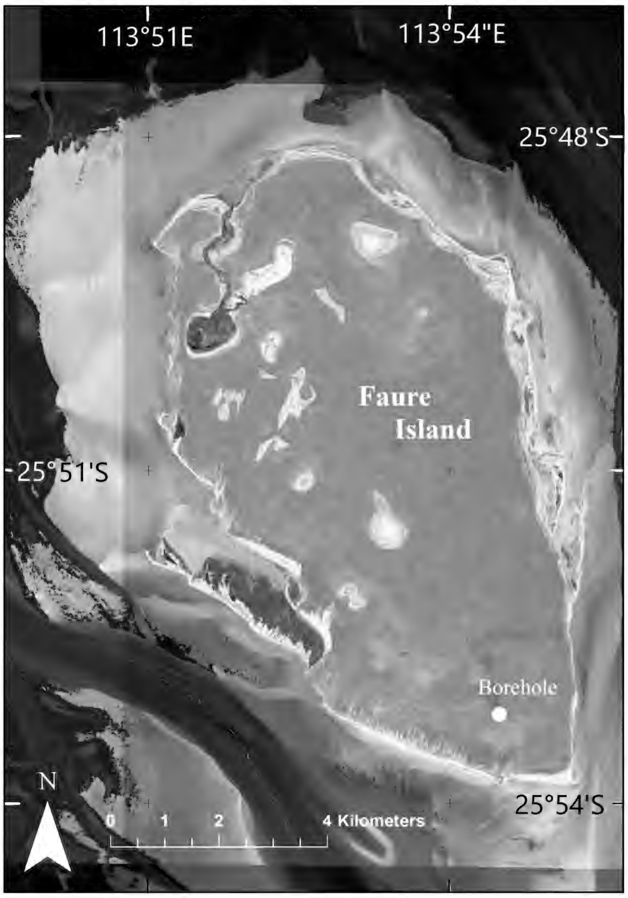

Figure 2. Faure Island showing extensive sand flats, which are exposed at low tide, the position of mangroves and the position of the bore.

As of 2008, feral predators and domestic grazers were removed, except for a small number of sheep *Ovis aries*, one horse *Equus caballus* and the house mouse *Mus musculus* (McCluskey 2008; Algar *et al*. 2010). There are no large kangaroos (*Macropus* spp.). Critically endangered marsupial species, such as the boodie *Bettongia lesueur*, have been re-introduced (McCluskey 2008).

The bore, which draws water from the Carnarvon Artesian Basin, is now partly saline. It is positioned above the northern and western extremity of the Mulga/Eucalypt Line (Mulga *Acacia aneura;* Fig. 1). Ground water on the Mulga side of this line is generally fresh—which has aided the development of the pastoral rangelands—whereas ground water on the Eucalypt side is generally saline (Serventy & Whittell 1976). Storr (1985, 1990) highlighted that the line provides a demarcation in range for many bird species, whereas Johnstone *et al*. (2000) point out that much of the avian diversity in the region stems from the intermixing of the avifaunas from either side.

The Mulga/Eucalypt Line is a natural ecotone that demarcates the acacia-dominated Eyrean vegetation of the north and inland from the eucalypt-dominated vegetation of the south-west (Taylor 1926; Serventy & Whittell 1976; Johnstone *et al*. 2000). Faure Island is situated marginally on the drier Eyrean side, as well as being positioned at the overlap zone of the summer and winter rainfall convergence zone (see *Climate* below) and in the Carnarvon Bioregion ~36 km above the boundary with the Yalgoo Bioregion (Fig. 1).

The Mulga/Eucalypt Line bisects Shark Bay whereas the Carnarvon and Yalgoo bioregions both bisect the southern Peron Peninsula, in Nanga, to the southwest of Faure Island. The Australian bioregions are defined by their climate, lithology/geology, landform, vegetation, fauna, and land use (Department of Environment and Energy 2018).

Ecotones in general show greater species richness and allele divergence than their immediate surrounding areas (Odum 1953; Smith *et al*. 1997; Kark & Van Rensberg 2006). In contrast to large land areas, islands in general show diminished species richness and harbour morphological variants diverged from adjacent mainland communities, although the extent of species richness depends on the island's size (MacArthur & Wilson 1967; Ford 1989). Thus, the positioning of Faure Island within a large and significant ecotone and its isolation as an island may synergistically interact to provide unique outcomes in relation to genetic variations and ecological associations in its assemblage of terrestrial bird species.

Climate

The climate is semi-arid to arid, with hot summers and mild winters. Precipitation is erratic falling mainly in winter with an annual average of 224.5 mm, recorded at Denham (~35 km to the west) over 1883–2009 (Bureau of Meteorology 2009). Cyclones can bring significant precipitation in summer and autumn (Hancock *et al*. 2000). Most of the year Faure Island receives modest rainfall and is thus more arid than the average suggests. Faure Island is also situated in the summer/winter rainfall convergence zone (Johnstone *et al*. 2000). Many northern birds have their ranges limited by the southern extent of summer rain. Conversely, the northern range of many southern birds is limited by the extent of the northern reach of winter rains (Blakers *et al*. 1984; Storr 1990; Johnstone *et al*. 2000; Barrett *et al*. 2003). Just prior to the current study, precipitation at Denham was measured at 6.8 mm for October and November 2008, including 2.0 mm that fell on 6 November 2008 (Bureau of Meteorology 2009). No ephemeral ground water was detected during the study and all birridas (seasonally inundated gypsum saltpans) observed from the ground and air were dry.

Vegetation

The vegetation surrounding the watering point has been severely modified by a long history of heavy and sustained grazing pressure of sheep, and the introduced Buffel Grass has established as a dense permanent ground layer replacing much of the former understorey. Formerly, the community would have been an *Acacia* shrubland, dominated by Kurara *Acacia tetragonophylla* and Horse Mulga *A. ramulosa* with a seasonal understorey dominated by short-lived perennial and annual species from the Poaceae, Asteraceae and Chenopodiaceae families. Isolated individuals of non-indigenous tree species established around the watering point include Athel Tree *Tamarix aphylla*, Moort *Eucalyptus platypus* and Date Palm *Phoenix dactylifera*.

On the western side of the island are two large regions of Grey Mangroves *Avicennia marina* with many smaller stands around the Island's perimeter, from significant clumps to single trees (pers. obs). Grey Mangroves are also present at the northern end of Peron Peninsula (Johnstone 1990; Storr 1990; Johnstone *et al.* 2000). The Carnarvon and Shark Bay regions represent the most southern extent of mangroves that support mangrove-specific birds (Johnstone 1990).

Piosphere

A piosphere is the zone around a watering point that shows the greatest damage from grazing and the trampling of hoofed mammals (Osborn *et al*. 1932; Lange *et al*. 1969). Although typically circular, it can be any shape especially if fences or buildings restrict access. It is clearly visible from aerial photographs, but the damage becomes more subtle and harder to detect farther from the watering point where the effects are then more related to selective grazing rather than general overgrazing and physical damage (Landsberg *et al*. 1997; James *et al*. 1999).

The piosphere surrounding the Faure Island bore measured ~275 m radius, from 355° clockwise to 245° (a total 250°; ~16.5 ha) owing to fencing that restricted grazing. The extent of the piosphere was measured using Google Earth images from an 'eye-altitude' of 900 m.

METHODS

Taxonomic procedure

Taxonomy of birds follows Christidis & Boles (2008). Scientific names of bird species are given in Tables 1 and 3 and at their first mention in the text. Plant names follow FloraBase (2009). This study was undertaken in November 2008.

Surveying and monitoring

The bore was monitored from 15:30–18:30 on 14 November 2008, and from 07:30–11:00 and 15:30–18:00 on 15 November 2008. In addition, ~15 km of the island's perimeter was surveyed for birds and 11 inland crossings of the island were made over four days on the 11–13 and 16 November 2008.

A natural hide formed by a small *Eucalyptus* sp. ~30 m from the bore was used to monitor birds coming and going from the bore and to view birds perching in the larger trees within a 200 × 200 m (2 ha) quadrat, centred on the bore. All birds here were counted and recorded as they entered the piosphere or in the case of the Zebra Finch as they approached the water.

Birds were categorised as either extending across the island, in the immediate ~100-ha zone around the bore, or birds that foraged within the piosphere, which includes birds that drank at the bore. Birds were determined to be foraging or drinking by their actions. Observations of birds within 100 ha of the bore were made daily, by driving, at ~10–15 km/hr, through the area (n = 11) or by

searching ~10 ha around the homestead for two hours at a time (n = 6) and walking transects (~1.3 km) to the bore (n = 6) and recording the birds seen. Birds were observed during inland crossings of the island (n = 11) while standing in the back of a 4WD utility enabling 360° observations. The vehicle was stopped when necessary to identify birds. Birds detected across the whole island and from within the 100-ha zone were recorded in relative abundance categories at the end of each day. Thus there are no absolute abundance counts for these data. Only birds seen at the bore and in the piosphere were recorded as absolute counts. Where absolute and relative data are compared they are all reported as categories of abundance.

Analyses

Geographical distribution for each terrestrial species was categorised using relative abundances at the bore and piosphere, the 100-ha zone around the bore and the whole island. Therefore, it was possible to detect gradients or patterns of abundance and determine if species abundances were either higher or lower with regard to the proximity of the piosphere. The nullifiable (H_0) hypothesis was that the bore has no effect on the geographical distribution of each bird species on Faure Island. However, the probability of incurring Type I or Type II errors in these analyses was high, because sample sizes for some species were low.

RESULTS

In total, 1625 birds from 11 species were recorded in the 2-ha quadrat around the bore (Table 1). Only four of these drank at the bore: the Crested Pigeon, Welcome Swallow *Hirundo neoxena*, Tree Martin *Petrochelidon nigricans* and Zebra Finch. Zebra Finches attended the bore, in the greatest numbers, each day. Zebra Finch abundance increased during the day as the temperature rose and decreased in the late afternoon as the temperature fell (Fig. 3a). The Zebra Finch is a flocking bird detected over the entire island. It was frequently seen in flocks of 5–50 as they approached the bore. These smaller flocks accumulated into larger flocks, of up to 300 plus

Table 1
Counts of individuals observed in the 2-ha quadrat surrounding the artificial watering point; the asterisk (*) denotes species that drank at the bore. The Spiny-cheeked Honeyeater is omitted from this table, because its numeric count was not recorded; this was an oversight during fieldwork.

Common name	Scientific name	Totals
Crested Pigeon*	*Ocyphaps lophotes*	104
Brown Goshawk	*Accipiter fasciatus*	3
Wedge-tailed Eagle	*Aquila audax*	1
Brown Falcon	*Falco berigora*	3
Sacred Kingfisher	*Todiramphus sanctus*	1
Singing Honeyeater	*Lichenostomus virescens*	12
White-breasted Woodswallow	*Artamus leucorynchus*	3
Grey Butcherbird	*Cracticus torquatus*	1
Little Crow	*Corvus bennetti*	2
Welcome Swallow*	*Hirundo neoxena*	50
Tree Martin*	*Petrochelidon nigricans*	9
Zebra Finch*	*Taeniopygia guttata*	1437
Total		1626

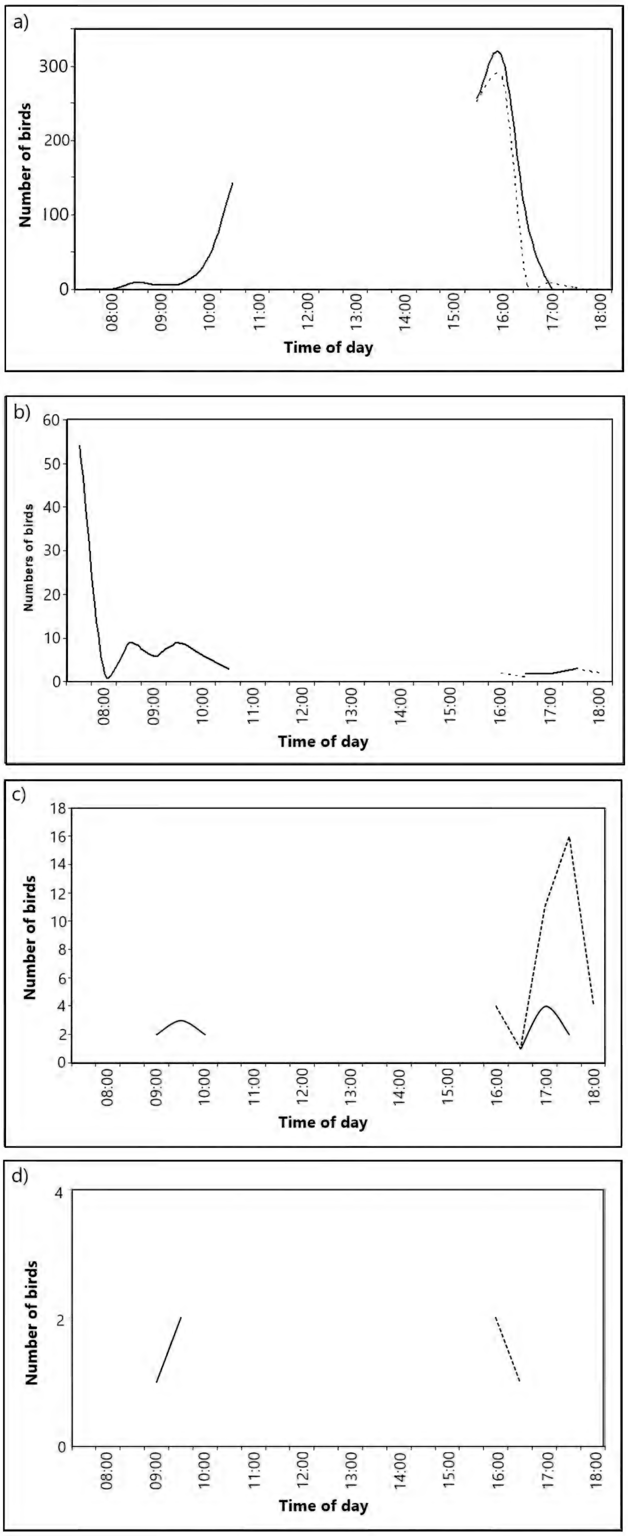

Figure 3. Abundances and temporal patterns of drinking recorded in this study: a) Zebra Finch; b) Crested Pigeon; c) Welcome Swallow; and d) Tree Martin. The dash line is the first day of monitoring (14/11/2008) and the solid line is the second (15/11/2008). The morning of the first day and the middle of both days over 10:30–14:30 were not monitored.

birds, near the bore, inside the piosphere, but in the cover of *Acacia* shrubs. Crested Pigeons were in greatest abundance early in the morning and showed no trend associated with increasing temperature throughout the day (Fig. 3b, Table 2). Welcome Swallows showed small peaks in abundance in the morning and afternoon, and a more abrupt peak on the afternoon of November 14 (Fig. 3c). Tree Martins were recorded at two of the three monitoring periods (Fig. 3d). In addition, the White-bellied Sea-Eagle *Haliaeetus leucogaster* has been reported drinking from the water troughs, in the early mornings of the survey period (Jo Williams, Australian Wildlife Conservancy, pers. comm. Nov. 2008).

Other birds were recorded in the 2-ha quadrat around the bore, although they were not observed drinking. These include a juvenile Brown Goshawk *Accipiter fasciatus*, Sacred Kingfisher *Todiramphus sanctus* and Singing Honeyeater *Lichenostomus virescens* perched in larger trees that are close to the bore. The Brown Goshawk may have used them as cover from which to ambush prey whereas the other two species used them as a high perch for calling. The Little Crow *Corvus bennetti* and Grey Butcherbird *Cracticus torquatus* were opportunistically recorded in the 2-ha quadrat while driving past. The Wedge-tailed Eagle *Aquila audax*, Brown Falcon *Falco berigora* and White-breasted Woodswallow *Artamus leucorynchus* were seen flying over the 2-ha quadrat, but they did not fly directly over or within 50 m of the water troughs.

There were 18 species detected in the 100-ha zone inclusive of the piosphere. Bird distribution patterns (including gradients) were identified when abundances in the piosphere were compared with the 100-ha zone and the whole island. Of the species recorded in the piosphere, 35% (n = 7 species) were detected in lower abundance than elsewhere on the island, 45% (n = 9 species) in higher abundance and 20% (n = 4 species) showed no change in abundance. Thus 80% of bird species showed a change in their distributive abundance at the piosphere and bore, compared with the surrounding 100-ha zone and the whole island (Table 3). Notably, only two species were common in the piosphere without going to drink water: the Singing Honeyeater and the Spiny-cheeked Honeyeater *Acanthagenys rufogularis*.

DISCUSSION

This survey provides a snapshot of how birds used this artificial habitat. The data do not demonstrate how birds might use the bore either seasonally or during migration, or how nocturnal birds use watering points (see Cameron 1938; Davies 1972). However, resident birds dependent on this water source for diurnal use would be detected in this short temporal survey. Possibly some birds may have been counted twice, though with diminishing probability when fewer birds were present.

Birds at the watering point: overview

Five bird species were recorded drinking at the bore. Four of these species are known to have increased in range and numbers throughout Australian rangelands with the addition of artificial watering points: White-bellied Sea-Eagle, Crested Pigeon, Welcome Swallow and Zebra Finch (Fisher *et al*. 1972; Davies & Chapman 1974; Davies 1977a; Blakers *et al*. 1984; Curry & Hacker 1990; Saunders & Curry 1990; Reid & Fleming 1992; Landsberg *et al*. 1997; Johnstone *et al*. 2000; Shephard *et al*. 2005; Olsen *et al*. 2006a). However, the fifth species, the Tree Martin has not been reported (by the same authors) demonstrating any range change associated with the spread of artificial watering points. It has been identified previously as a passage migrant at the island, sometimes in extensive flocks (Dell & Cherriman 2008). The provision of drinking water may dictate this section of its migration pathway.

Drinking patterns

The Crested Pigeon and Zebra Finch are granivorous birds and the Welcome Swallow and Tree Martin are aerial insectivores. Landsberg *et al*. (1997) found that granivores drink most frequently, because grain provides

Table 2
Bird species presence recorded hourly over two days (x = present). Times given are at the end of the hour. Sunrise = 06:28 and sunset = 19:50; temperature min 17.5°C (15 Nov.) and max 27.5°C (14 Nov.)

	14-Nov-08				15-Nov-08						
Species and time	**15:30**	**16:30**	**17:30**	**18:00**	**7:30**	**8:30**	**9:30**	**10:30**	**15:30**	**16:30**	**17:30**
Crested Pigeon	x	x	x	x	x	x	x	x		x	x
Brown Goshawk				x	x			x			
Wedge-tailed Eagle								x			
Brown Falcon								x			
Sacred Kingfisher				x							
Singing Honeyeater	x					x	x				
White-breasted Woodswallow							x				
Little Crow									x		
Welcome Swallow	x	x	x	x		x	x			x	x
Tree Martin	x	x	x			x	x	x			
Zebra Finch	x	x	x			x	x	x	x	x	

Table 3

The relative abundances of terrestrial bird species detected within the piosphere (includes birds coming to drink), the 100-ha zone around the watering point and across the whole island. The latter are not intended to be a complete list of terrestrial birds on the island. Birds flying over an area are included in that area.

Species	Island	100-ha	Piosphere	Pattern
Crested Pigeon *Ocyphaps lophotes*	C	A	C[1]	↑
White-bellied Sea-Eagle *Haliaeetus leucogaster*	U	R	U[1*]	↑
Brown Goshawk *Accipiter fasciatus*	U	U	U	↔
Wedge-tailed Eagle *Aquila audax*	U	U	R	↔ II (↑)
Brown Falcon *Falco berigora*	U	U	R	↔ II (↑)
Sacred Kingfisher *Todiramphus sanctus*	R	R	R	↔
White-browed Scrubwren *Sericornis frontalis*	U	U	A	↓
Redthroat *Pyrrholaemus brunneus*	C	C	A	↓
Pied Honeyeater *Certhionyx variegatus*	A	C	A	↓
Singing Honeyeater *Lichenostomus virescens*	C	C	C	↔
Spiny-cheeked Honeyeater *Acanthagenys rufogularis*	C	C	C	↔
White-breasted Woodswallow *Artamus leucorynchus*	C	U	R	↓
Grey Butcherbird *Cracticus torquatus*	A	A	R	↑
Little Crow *Corvus bennetti*	R	R	U	↑
Yellow White-eye *Zosterops luteus*	U	U	A	↓
Silvereye *Zosterops lateralis*	U	U	A	↓
Welcome Swallow *Hirundo neoxena*	C	U	U[1]	↔ II (↑)
Tree Martin *Petrochelidon nigricans*	C	U	U[1]	↔ II (↑)
Zebra Finch *Taeniopygia guttata*	C	C	C[1]	↑
Australasian Pipit *Anthus novaeseelandiae*	C	C	A	↓

Notes: C = common (seen in all surveys), U = uncommon (seen more than once, but not in all surveys), R = rare (seen once) and A = absent (not observed). [1] indicates the species entered the piosphere to drink; * is a pers. comm. from Jo Williams. ↑ = increasing and ↓ = decreasing relative abundance, closer to the piosphere. ↔ indicates that the species abundance may not be affected by the bore and piosphere. II indicates a Type II error. Corrected results after committing Type II errors are given as increasing (↑), and are probably artefacts due to small sample sizes.

little water content. In contrast, insectivorous birds are the least dependent, obtaining most of their water from insects (Fisher *et al*. 1972). This study also detected the predictable pattern of abundance with granivorous birds dominating counts at the bore: 1541:104 individuals (Table 1).

Davies (1972) found that Crested Pigeons preferentially drank early in the morning, more Zebra Finches drank in the hottest part of the day and Welcome Swallows drank in the morning and afternoon. Results that match with temporal drinking patterns observed in this study. However, Fisher *et al*. (1972) found Tree Martins drank throughout the day whereas this study detected them drinking only at either end of the day.

White-bellied Sea-Eagles are attracted to water in the inland, because this is where they get virtually all of their live prey, which consists primarily of fish, waterbirds and turtles (Fleay 1948; Olsen *et al*. 2006a, b; Debus 2008). On Faure Island, this species may only use the bore for drinking and bathing, because its main prey of fish and waterbirds are more abundant at beaches, tidal flats and lagoons (pers. obs).

Birds with greater abundances at the bore and piosphere

The bore and the piosphere influenced the geographical distribution of terrestrial birds on Faure Island. Eighty percent of the birds studied showed a change in relative abundance between the piosphere and bore compared with the 100-ha zone around the bore and the whole island. The availability of reliable drinking water had direct and indirect influences on the geographical abundance of terrestrial birds on the island.

Raptors are likely to be attracted to a bore (or other features) that concentrate prey animals (Olsen 1995; Aumann 2001; Shephard *et al*. 2005; Fulton 2006). At the time of this survey goats (*Capra hircus*) had been eradicated and sheep numbers had been significantly reduced on the island (Burbidge & Morris 2002). In the absence of the young of these mammals, raptors, particularly the Wedge-tailed Eagle, may preferentially hunt the re-introduced marsupials at the bore. Notably, Wedge-tailed Eagles adapted their diet to birds including the Plains Wanderer *Pedionomus torquatus* when rabbit (*Oryctolagus cuniculus*) numbers were reduced by the release of haemorrhagic disease Rabbit *Calicivirus* (Sharp *et al*. 2002; Fulton 2019a).

The Brown Goshawk was the most commonly detected raptor, recorded three times in the piosphere. This species is uncommon to rare in Shark Bay (Davies & Chapman 1974; Johnstone *et al*. 2000), although more common at watercourses and mangroves where it uses larger trees to perch (Johnstone *et al*. 2000). The bore may provide an important habitat component for the Brown Goshawk on Faure Island. A goshawk nest was detected within the 100-ha zone and a juvenile was observed

moving from the area of the nest to the bore, indicating it may have fledged from that nest. Future research could involve searching the nests and surrounds near the bore for evidence of skeletal remains, to learn if the Brown Goshawk is depredating re-introduced marsupials.

Other predatory birds showed a response to the bore: Little Crows were detected in the quadrat three times, but were not seen drinking, although their proximity and behaviour at the water troughs indicated that they may drink and bathe there. The Grey Butcherbird is a known predator of smaller birds (Pizzey & Knight 1997; Fulton 2008, 2018, 2019b). It may attend the bore due to the concentration of prey. Small birds, particularly the Zebra Finch, were plentiful at the bore. Individual birds, particularly juveniles that bathe, can become waterlogged and incapacitated and thus easy prey for cracticids and corvids (Debus *et al*. 2006; Fulton 2006).

Birds that drank at the bore and did not stay within the piosphere

Crested Pigeons flew out of sight after drinking (>100 m outside the piosphere) and were never recorded in the 100-ha zone, unless perched near the bore before drinking. Presumably, they were prepared to travel substantial distances to obtain water. Zebra Finches flew outside the piosphere to *Acacia* spp. They only accumulated in large numbers at the bore and piosphere before dispersing into smaller flocks over the island. Granivorous species did not feed within the piosphere, which may be related to the higher chance of predation through less cover and/or the lack of seed through over-grazing. The White-bellied Sea-Eagle and other raptors did not stay in the area. They have large hunting territories, although they are generally linked to inland water sources that provide them with prey (Marchant & Higgins 1993; Debus 2008). Aerial insectivores presumably move over the whole island in response to their aerial feeding.

Birds that did not drink but were common near the bore and piosphere

Davies (1972) found that many of the same birds, as this study, approached the vicinity of watering points but did not drink (Table 1). However, the Spiny-cheeked and Singing Honeyeaters were the only birds commonly detected in the piosphere that did not attend the watering point. These two species were common in the 100-ha search zone around the bore and across the whole island; they are considered open-country birds and are common in arid lands (Blakers *et al*. 1984; Barrett *et al*. 2003). Schneider & Griesser (2009) reported that Singing and Spiny-cheeked Honeyeaters are found in moderate abundances (more so than the Pied Honeyeater *Certhionyx variegatus*) at watering points, but they failed to connect the need to drink and simply correlated the proximity of birds and species richness to watering points. Fisher *et al*. (1972), in contrast to my findings, found that large numbers of Spiny-cheeked Honeyeaters came to drink. Fisher *et al*. (1972) recorded 1500–2000 Spiny-cheeked Honeyeaters coming to drink, on one day, from all directions during a two-hour period. They also found that they drank at all periods of the day, but predominantly in the first two hours after sunrise.

Singing Honeyeaters have been reported at natural waterholes, and at equal frequencies at artificial lakes and control dry desert sites, indicating that they do not simply congregate at water (Schneider & Griesser 2009). This study did not detect them drinking at the bore, although they were common in the piosphere. The Singing Honeyeater is broadly distributed and abundant across Australia, including in the most arid regions (Barrett *et al*. 2003); however, there is little information as to its physiological adaptations to extreme arid environs. Notably, it was found abundant throughout the Great Victoria Desert when conditions were very dry—when rock holes and deep depressions were dry for months and the 'spinifex' had a dead appearance throughout the desert (Ford & Sedgwick 1967). Brooker *et al*. (1979) surveyed birds in the Nullarbor (1967–1978), which is climatically desert with no permanent natural surface water; yet they found the Singing Honeyeater abundant at all sites throughout their study. Physiologically, Skadhauge (1974) found that the Singing Honeyeater's renal concentrating ability compared favourably with other arid-adapted species such as the Zebra Finch. However, it has the added advantage over most granivores to gather its metabolic water requirements from invertebrates and nectar. The wide range of habitats occupied by the Singing Honeyeater suggests that further research into its physiology may provide interesting results with possible physiological adaptations, which may be evident clinally across Australia.

Birds more common away from the bore and piosphere

The Redthroat *Pyrrholaemus brunneus*, like the White-browed Scrubwren *Sericornis frontalis*, has most likely been excluded from the piosphere by overgrazing eliminating cover and its preferred invertebrate prey (Ambrose & Davies 1989; Rowley & Russell 1997; Higgins & Peter 2002). Australasian Pipits *Anthus novaeseelandiae* were frequently detected in the 100-ha zone and across the whole island, although they were absent from the piosphere. This species generally proliferates in grazed areas, feeding on invertebrates such as beetles (Coleoptera), grasshoppers (Orthoptera), ants (Hymenoptera) and springtails (Collembola; Garrick 1981; Fulton & Majer 2006; Higgins *et al*. 2006). James *et al*. (1999) suggested that some invertebrates (as above) have been replaced at bores by invertebrates that have aquatic instars. The absence of the Australasian Pipit in the piosphere, although common elsewhere on Faure Island, suggests that the invertebrates it feeds on were unavailable there, perhaps giving some support to the findings of James *et al*. (1999).

Future research might investigate what birds frequent the bore if it is shut down and monitor the recovery of vegetation and invertebrates in the absence of trampling at the bore by live stock.

CONCLUSION

The null hypothesis that the bore has no effect on the concentration of birds on the island is rejected. Because this study was limited in time and scope it is important to view the results in line with the limitations. Water was used by some species more than others. It is likely

that there will be opportunistic predation on introduced marsupials and birds at the bore, particularly when they are more concentrated there.

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A.R. Wallace in the light of historical method

JOHN VAN WYHE

National University of Singapore

✉ *dbsjmvw@nus.edu.sg*

ABSTRACT

Over the past fifty years the now well-known story of the great Victorian naturalist Alfred Russel Wallace has transformed to one very different from that familiar during his lifetime and for decades after his death in 1913. The new Wallace story is attractive and inspiring in many ways. It sells well and infuses many with a sense of purpose, but that it has changed so much remains unknown. This transformation is due largely to most writers on Wallace since the 1960s not having been trained as historians. Whereas some modern writers on him are seen as conspiracy theorists, most have simply followed what has been written or broadcast about him in recent decades. Unwittingly, however, this has culminated in a story of Wallace incompatible with historical method and contextual analysis.

Keywords: Wallace, Darwin, biography, historiography, history of science

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INTRODUCTION

Stories about the great Victorian naturalist Alfred Russel Wallace (1823–1913) that appear today are remarkably consistent. What remains unknown, however, is how different the modern stories are from those told by his contemporaries and writers for the half century following his death. Popular themes in the modern Wallace story include:

1. Wallace was working-class or from the opposite side of the social spectrum than Charles Darwin;
2. As a youth Wallace was forced to leave school early at age 14 because the family money ran out;
3. He went to the Amazon with H.W. Bates to 'solve the problem of the origin of species';
4. He later went to the Malay Archipelago on the same quest;
5. An overarching goal during these journeys was to discover the 'mechanism' for evolution;
6. On the Moluccan island of Halmahera, he derived the idea of natural selection from the population theory of Thomas Malthus (just as Darwin had);
7. His evolutionary theory written in 1858 was identical to Darwin's;
8. Wallace wrote this essay in order to send it to Darwin;
9. When Darwin said he received the essay seems doubtful or impossible because another letter Wallace sent at the same time to someone else arrived in England earlier than Darwin claimed to have received his;
10. Darwin's colleagues published Wallace's essay without his consent;
11. They put Darwin's contribution first which robbed Wallace of his priority;
12. Nevertheless, for decades it was known as the Darwin–Wallace theory of evolution;
13. Wallace was the greatest field biologist of the 19th century;
14. He is also the father of biogeography;
15. His book *The Malay Archipelago* has never been out of print;
16. At the end of his life he was the most famous scientist in the world; and
17. He has become strangely forgotten.

Everything in the above list is historically incorrect. The aim of this paper is to provide a more accurate understanding of Wallace by using rigorous historical methods.

DISCUSSION

Although abundant evidence and historical arguments exist to explain each of the points listed above, the following discussion of each illustrates the difference between accounts that follow historical method and those that promote the hero-underdog Wallace, whose fame or credit must be resurrected.

1. This view of Wallace emerged in the 1960s–1970s. Wealth was not the determiner of class identity in the 19th century—Wallace and his family were middle class. His father trained as a solicitor and was listed as a 'gentleman' on Wallace's birth certificate. The house where Wallace was born is sometimes compared to the *much* larger and grander house where Darwin was born. Nevertheless, Wallace's detached house was the grandest in an area where the norm was peasant cottages or terraced houses. Darwin and Wallace were not from opposite ends of the social spectrum, but from different parts of the

middle class, and so had more in common than social differences.

2. This was first put forward in 1980. Wallace left school at the normal leaving age of 14. After all, he was qualified to later become an assistant teacher in Leicester. This error derives from Wallace's autobiographical description (Wallace 1905; van Wyhe 2012) of his family's financial situation in his final school phase and modern popular writers unaware of the leaving age for schoolboys in England during the Victorian period.

3. Wallace went to the Amazon to work as a specimen collector. He always said so, both at the time, and in later life. All the historical evidence supports this and there is no evidence, that he went to discover evolution or pursued any such activity while there (van Wyhe 2014), except for one apparent piece. At the start of his 1863 book *The Naturalist on the River Amazons*, H.W. Bates published a modified version of an 1847 letter from Wallace that said nothing about an expedition. Bates claimed that Wallace wrote that they should go on an expedition 'towards solving the problem of the origin of species'. (Bates 1863, vol. 1, p. 3). By comparison, the original letter, states: 'I should like to take some one family [of insects in England], to study thoroughly, principally with a view to the theory of the origin of species' (Wallace 1905, pp. 256–7). Portraying Wallace as motivated to travel to the Amazon to solve a problem of species has became increasingly popular in recent years.

4. The belief that Wallace then went to the Malay Archipelago on the same quest is based on the above error and has no contemporary evidence to support it. He wrote, at the time and later, that he went to be a specimen collector—a task at which he was enormously successful. To describe a figure as on a quest to solve a great scientific mystery is nearly always naïve given that historians of science have repeatedly found that such claims are romanticised retrospective accounts, and not how science normally transpired.

5. There is no evidence that Wallace was searching for any mechanism or solution. In contrast, his writings from the Malay Archipelago at first ridicule the idea of adaption or that every feature of an organism had a purpose. This was probably based on his contempt for natural theology with its stress on the providential design of living things. For example, he argued that the large canine teeth of orangutans served no purpose (Wallace 1856, p. 29). Wallace already believed that living things changed over time, but adaptation was not yet part of his thinking. Only after the publication of Charles Darwin's *Origin of Species* (1859), did Wallace describe his earlier activities as searching for the solution to a problem. Wallace seemingly adapted to a widespread shift in language following Darwin's book, in which a solution to the problem was presented. Thereafter thousands of writers began to refer to 'the' problem of the origin of species. Thus this is a post-1859 manner of speaking. It is the essence of historical understanding to distinguish between retrospective re-tellings and contemporary evidence as to what occurred. Modern writers typically use the word 'mechanism' in this context (i.e. Wallace was searching for the 'mechanism') but such language emerged only around 1900. Yet this way of describing Wallace as on a long-term quest to solve the problem of species is becoming ever more common in writings about him.

6. Wallace conceived of natural selection and wrote his essay on the island of Ternate in February 1858. The error of believing he was on the neighbouring island of Gilolo/Halmahera is the result of fallacious reasoning by H. Lewis McKinney (1972). He concluded that because Wallace wrote in a 25 January letter that he planned to go to Halmahera in about a week, that he must therefore have done so. However, the only dated document from that time, (February 1858) is the essay itself, which is signed and dated 'Ternate' (van Wyhe 2013, pp. 202 ff). Evidence from the time and place outweighs any projection of future plans. Trying to explain what seemed an anomaly, many writers have invented explanations for why the essay was signed Ternate if it was actually written on Halmahera. For example, several writers have claimed that he signed it with his postal base (Ternate). Not only was this contrary to the convention of writers in the 19th century, but Wallace's other surviving documents are all signed according to his actual location, never according to the nearest post office. Furthermore, Wallace always recounted that he had conceived of natural selection and written his essay in his house on Ternate.

   Another example of Wallace retelling his story is that Malthus's (1826) theories are only mentioned in his later recollections *after* he had read Darwin and his mention of Malthus. Therefore, this is not independent evidence and insufficient to conclude that Wallace thought of Malthus in 1858. There is no mention of Malthus in Wallace's Ternate essay. The Malthus-like statements are based on his copy of Charles Lyell's *Principles of Geology* (1835), such as 'the tendency of population to increase beyond the means of subsistence' and 'In the universal struggle for existence, the right of the strongest eventually prevails' (Lyell 1835, vol. 3, pp. 94–95 and p. 9), which Wallace had with him when he wrote his essay. If Wallace also thought of Malthus, which he may have done, there is no contemporary evidence of this. Nevertheless, this has not prevented modern writers telling the story according to Wallace's later, and historically unreliable, recollections.

7. Wallace's original theory was in some ways similar and parallel to Darwin's, but also quite different. The more historians of science have analysed it over the past decades, the more differences emerge (Bowler 1984; Ruse 1996; Kottler 1985; van Wyhe 2013, pp. 208 ff).

8. Wallace *recollected* decades later that he wrote the essay 'in order to send it to Darwin' (Wallace 1905, vol. 1, p. 363). However, the only evidence we have for his original intentions is an 1887 letter: 'I *had* the idea of working it out, so far as I was able, when I returned home' (Wallace 1887). Although a recollection, it conforms with Wallace not sending

his essay to anyone on the following monthly mail steamer in March. Only after he received a letter of high praise from Darwin (on the March steamer) mentioning that Charles Lyell also thought highly of his earlier work, did Wallace send the essay to Darwin by the following, April, mail steamer—requesting that it might be forwarded to Lyell who was the main opponent addressed in the essay. (van Wyhe & Rookmaaker 2012)

9. This belief also traces back to McKinney (1972) who found a letter to someone else that arrived in England two weeks earlier than Darwin's and *assumed* that the letter to Darwin must have been sent at the same time. McKinney's (1972) assumption that they were sent the same day launched decades of fruitless speculation. Wallace was replying to the letter from Darwin that arrived on the March steamer. This was part of a sequence of letters from (and replying to) Darwin, not one written out of sequence to Darwin that was not a reply. Wallace's reply and his Ternate essay went on the following April steamer. The mail connections from that date arrived in London exactly on 17 June 1858—these connections have all been verified and there is no scope to consider them as uncertain or conjectural, and Darwin's home was one day by post from London. Darwin wrote to Lyell on the 18th saying he had received an essay from Wallace that day. There is no mystery and only failure to follow correct historical practice ever introduced the mistaken notion that there was one. (van Wyhe & Rookmaaker 2012; van Wyhe 2013, pp. 220 ff)

10. Wallace's essay was published in accordance with the standards of the day. The notion that it was done 'without consent' was created by Beddall (1968) and launched decades of repeated assertions to this effect. Conventions of the day dictated that only if the essay had been marked 'private' or not for publication would any rules have been broken. Hence, Wallace was aware that it could be published if the recipients, especially the great geologist Charles Lyell, thought proper. Wallace expressed no surprise that it had been read before the Linnean Society in his 6 October 1858 letter to his mother: 'I have received letters from Mr Darwin & Dr Hooker two of the greatest most eminent Naturalists in England which has highly gratified me. I sent Mr Darwin an essay on a subject in which he is now writing a great work. He shewed it to Dr Hooker & Mr Darwin Sir C Lyell, who thought so highly of it that they immediately read it before the 'Linean Society'. This insures me the acquaintance and assistance of these eminent men on my return home' (van Wyhe & Rookmaaker 2013, p. 180).

11. Wallace's and Darwin's contributions were communicated by Charles Lyell and Joseph Dalton Hooker to the Linnean Society on 1 July 1858 'in the order of their dates' (Darwin & Wallace 1858, p. 45). However, there was no singular 'priority' in Victorian science. At least three types were widely recognised in the 19th century. Darwin already had two of the three: 1) the first to conceive of an idea and 2) the first to share an idea with colleagues. Darwin shared the third form of priority equally with Wallace, i.e. the first to publish. The idea of a unitary 'priority' issue between Wallace and Darwin is derived from modern conventions about publication and priority in science. Even if Wallace's paper had been published on its own ahead of Darwin, it was already known that Darwin had conceived of the idea and shared it with colleagues long before.

12. It was seldom described as the Darwin–Wallace theory of evolution because their joint papers were almost unknown compared to Darwin's controversial and internationally discussed *Origin of Species*. Furthermore, 'the theory' is an oversimplification since the *Origin of Species* contains more than the idea of natural selection. 'The theory' discussed by their contemporaries consisted of a host of elements that Wallace had never thought of such as sexual selection and recapitulative appearances in embryology. Contemporary discussions of the *Origin of Species* seldom referred to it as a theory that emanated equally from both men.

13. To say that Wallace was the greatest field biologist of the 19th century is meaningless hyperbole. This flattering title goes back to 1959 but only became common after a popular science book by David Quammen (1997).

14. Wallace was first described as founding 'the science of zoogeography' by zoogeographer and Wallace biographer Wilma B. George in 1964. However, Wallace came two generations *after* the advent of biogeography or the study of 'geographical distribution' which has long been traced to Buffon (1707–1788) although others attribute it to Alexander von Humboldt (1769–1859). The bookshelves of Wallace's day already groaned under volumes on this subject before he began to write his classic *The Geographical Distribution of Animals* (1876).

15. Wallace's great work *The Malay Archipelago* (1869) was out of print from 1922–1962. (van Wyhe 2015). A reviewer of John Bastin's 1986 reprint remarked that Oxford University Press 'deserves our thanks for bringing this long out of print classic back into general circulation' (Harper 1988)

16. Wallace was given this title around the year 2000. A large number of interviews and obituaries in which Wallace was often described in such superlative terms was discovered and republished online by Charles Smith (2000a, b) even though Wallace was not even close to being so famous in his lifetime. The reverent statements by journalists and obituarists that someone was the 'most famous' or 'greatest' naturalist was also applied to many others at the time. Examples described with exactly the same words include such luminaries as Richard Owen, R.L.C. Virchow, William Crookes, T.H. Huxley, Nicola Tesla, Marcellin Berthelot, I.I. Metchnikoff and Madame Curie. Such rhetoric does not show that any of these scientists was *the most famous*, but that such language was commonly used by journalists to describe an eminent subject they were writing about. There are also many examples flatly contradicting the belief that Wallace was the most famous, such as a piece that ran in a San Francisco newspaper in 1900 entitled 'The fifty greatest men of the nineteenth century'. Under the heading 'scientists' were

Alexander von Humboldt, Charles Darwin, Michael Faraday, T.H. Huxley and Louis Pasteur (Anon 1909). Some of the historically verifiable candidates to such a title around 1900 would be Oliver Lodge, Lord Kelvin, Louis Pasteur, John Fiske, E. Ray Lankester, Luther Burbank, Francis Galton or William Crookes.

17. The idea that Wallace is forgotten is the most fundamental and widely believed feature of Wallace today. Wallace is no more forgotten than dozens of other prominent men of science of the later 19th century. Almost all of the others are far less well known now than Wallace is. Wallace's fame is far greater than most other 19th-century naturalists. New books and articles on him appear every year.

    Whereas everyone familiar with Wallace agrees on what an admirable man he was—so curious, enthusiastic, intelligent, persevering, modest, good-humoured and a profoundly gifted observer of nature and more—that so many things written about him a century later are historically inaccurate has no bearing on his worth. So, how was the view of Wallace as a heroic-victim created in recent decades?

EARLY NARATIVES

It is unappreciated that Wallace's story was told during his lifetime and for 50 or so years afterwards in a greatly different way than it is today. For many years his accomplishments were celebrated but without any notion of his being forgotten, cheated, wronged or in any way being a figure for whom the record needed to be set straight, even though those writers had almost all of the historical evidence that we do. This proves that with the same evidence two radically different stories can be told—one following proper historical method and the other promotional literature. Although an entire volume could be filled with examples and explanations, the following instances serve to illustrate these dramatic differences.

In 1871 Darwin's brother, Erasmus, mentioned in a letter that 'in future histories of science the Wallace–Darwin episode will form one of the few bright points among rival claimants' (Litchfield 1904, vol. 2, p. 242). Their story was described as 'one of the brightest in the annals of science' (Woodall 1884). The American palaeontologist Henry Fairfield Osborn wrote in 1909 that 'the entire Darwin–Wallace history up to and including Wallace's noble and self-depreciatory tribute to Darwin on July 1 of last summer, is one of the brightest chapters in the history of science' (Osborn 1909, p. 328; 1928). When introducing Wallace in 1908, the President of the Linnean Society, Dukinfield Scott, remarked 'There is nothing in the history of Science more delightful or more noble than the story of the relations between yourself and Mr. Darwin, as told in the correspondence now so fully published—the story of a generous rivalry in which each discoverer strives to exalt the claims of the other' (Anon 1908, p. 4). In 1925, palaeontologist Richard Swann Lull described the story as 'a splendid act of chivalry for [Darwin] thus to bring forth the work of the younger man, but it did not in any way lessen Darwin's credit as the true discoverer and demonstrator of this important factor' (Lull 1925, vol. 1, p. 335.). Lull added 'At first, Darwin was inclined, out of chivalrous friendship for the young man, to suppress his own laboriously elaborated work and to publish Wallace's to the world. Fortunately the good counsels of his friends Hooker and Lyell prevailed and as a result a joint paper setting forth the views of both authors was read.' In 1952, the entomologist Arthur Ward Lindsey called it 'a fine example of cooperation and individual generosity' (Lindsey 1952, p. 27).

By 1980, however, Wallace's story was markedly different. The journalist Arnold Brackman claimed that the whole affair with Darwin was 'the greatest conspiracy in the annals of science', and that Wallace was the 'victim of a conspiracy by the scientific aristocracy of the day and was robbed in 1858 of his priority' (Brackman 1980, p. xi). Brackman, and zoologist and scientific administrator John Langdon Brooks (1984) wrote the first book-length conspiracy theories of Darwin vs. Wallace, plying accusations of lying, plagiarism and cheating against Darwin and his colleagues. In 1986 the American philosopher James Rachels, who specialised in ethics and animal rights—also with no training in the history of science—in an article entitled 'Darwin's moral lapse' called it a 'shabby affair' and a 'lamentable story of human weakness, in which some good men treated another good man disgracefully' (Rachels 1986). In 2000 Ghillean Prance, the President of the Linnean Society, wrote in a foreword to a new biography that Wallace was 'a 'forgotten naturalist' in comparison with the attention that has been given to Darwin's contribution. Various authors have sought to redress the injustice that befell Wallace and it is always good to welcome another book that seeks to set the record straight' (Wilson 2000). More recently, a trio of biologists opined that 'Wallace's contribution to the theory of evolution was not given the recognition it deserved and he was undoubtedly shabbily treated at the time' (Lloyd *et al*. 2010, p. 339). An article in *New Scientist* in 2013 by journalist Stephanie Pain declared 'the arrangement was as dodgy then as it would be now' (Pain 2013). Comedian Bill Bailey made a two-part BBC programme on Wallace in 2013, asserting in a tone of moral outrage 'they never even asked Wallace's permission to publish. The establishment were not going to let *their* man lose priority. So they cooked up this connivance…Wallace was robbed!' (Bailey 2013).

THE RISE OF VICTIM NARRATIVES

It was only in the late 1960s and 1970s that the original story of Wallace began to change. The first phase had nothing to do with Wallace but Darwin. In line with the values of those decades, a high-status, wealthy, privileged and immensely famous figure like Darwin was no longer acceptable or palatable to some. Some writers began to suggest that a forgotten, low-born figure was the true genius who deserved the fame and credit of the unfairly lauded Darwin. Other men were put forward as the overshadowed and forgotten victims from William Wells, James Prichard, William Lawrence and especially Edward Blyth and Patrick Matthew. Only then was Wallace cast in the same light with nearly identical claims made on his behalf. Whereas the other figures have mostly faded from view, Wallace has been written about ever since in ever stronger terms as truly great, truly disadvantaged,

and unfairly treated and forgotten. Making accusations against a famous and privileged figure on behalf of a supposedly disadvantaged and obscure underdog has become extremely attractive to many, quite apart from how accurate or inaccurate such claims might be. In the past 40 years, this theme pervades the literature on many historic figures—so primed are modern audiences to feel outrage at historical injustices that one need only make the accusation that a figure was a victim to win the moral high ground.

Some of the best-selling popular histories of science of recent decades make use of this theme. Well-known examples include John Harrison, the supposedly persecuted working-class hero of Dava Sobel's (1995) *Longitude*: *The True Story of a Lone Genius Who Solved the Greatest Scientific Problem of His Time*; William Smith, the working-class hero of Simon Winchester's (2001) best-selling *The Map that Changed the World*; and Brenda Maddox's (2002) *Rosalind Franklin: the Dark Lady of DNA* who, according to the book blurb, was 'airbrushed out of the greatest scientific discovery of the twentieth century'. Similarly, admirers of Nikola Tesla see him as an unfairly forgotten genius cheated out of his due fame and credit because of the fame and recognition given to mainstream Thomas Edison and Guglielmo Marconi. Recent accounts of Florence Nightingale and Mary Seacole parallel accounts of Darwin and Wallace. Nightingale was born into a wealthy family and because of her work training nurses and introducing a regime of hygiene and cleanliness in field hospitals during the Crimean War, and later in Britain, was recognised as the founder of modern nursing. Like Darwin, she became a household name in Victorian Britain. Mary Seacole was a mixed-race British Jamaican who travelled on her own to the Crimea where she set up the 'British Hotel' behind the lines for convalescent officers and treated many with traditional herbal remedies. Today she has a large and passionate following who believe that she, and not the privileged Nightingale, is the true hero. One could replace their stories with Darwin and Wallace's, so similar are the themes and claims even though Seacole played no role in modernizing the nursing profession.

The claim has become commonplace that Wallace did not become such a famous name as Darwin or that his fame has not survived as long because he was of lower social status. This idea also flies in the face of proper historical method. It is not enough to make an assertion—comparison must be made to others. Despite the elitism and overtly accepted social hierarchy of the time, there were many Victorian men of science from humble backgrounds who achieved towering reputations such as Humphry Davy, Michael Faraday, William Whewell, Adam Sedgwick, Richard Owen, David Livingstone, Herbert Spencer and T.H. Huxley, the latter born above a butcher's shop—a far humbler background than Wallace's.

Hagiography

To treat a figure from the history of science as a hero underdog needing resurrection goes against almost every principle of modern historical method. Historians rather contemptuously call such hero worship by journalists and popular writers 'hagiography'. Such writings sell well but these are not motives that lead to a dispassionate, critical and contextually nuanced account in which the evidence must form the basis of any assertion. Historians seek to understand what historical actors did and meant in terms of their own time and culture without overly apportioning praise or blame, even though book promotions and dust jackets etc. typically take literary license. Historians aim to challenge old-fashioned and uninformed histories and to add new information, elements or interpretations to earlier accounts. Similarly, Whiggish approaches, i.e. those treating the past as if it were an inevitable trajectory of progress and judging the past according to modern values and norms, have no place in rigorous historical analysis.

So great is the concern to not appear to be writing about a hero, Darwin scholars go out of their way to point out when Darwin was mistaken or to question the propriety of his behaviour—for example supposedly using his ill health as an excuse to avoid unwelcome guests or social activities and responsibilities. Another example is his labelling of his finch specimens in the Galapagos.

CONTEXTUALISM

One of the most powerful tools in the historian's toolkit is contextualism in which historical writings are interpreted according to an understanding of the period with an emphasis on the reconstruction of the actors' world. Students of the history of science learn how to read a work in this way as opposed to a naïve modern reading. Almost any historical document from the Bible to Shakespeare can be read by anyone today but, unless the original historical contexts are taken into account, their understanding will bear little relation to that of the original writers and readers. The constellation of ideas and issues they were addressing or silently referencing are significantly different from what a modern reading of one of their writings will produce—they were not taking part in a timeless debate about unchanging topics or questions

Timelessness is another refuted perspective. No historian of science could say that 'science works like X' without qualification. The science of the mid-19th century or the early 16th century or today are greatly different, so it is meaningless to say without qualification that in science, priority is established by X.

Actors' categories

Historians seek to understand what figures in the history of science were doing in terms of so-called actors' categories. One attempt to do this was seen when historians began to use the word 'transmutation' instead of evolution because the former term was used before the word evolution was used in its modern sense. However, use of 'transmutation' is widely imitated by non-historians without understanding why it is used and what it means. If a writer simply says that transmutation is what evolution was called in the past, this misses the point. The point is not vocabulary. If transmutation and evolution meant exactly the same thing then insisting on the term transmutation would be pointlessly pedantic and pretentious. The reasons historians often stress earlier terms is that they *did not mean* the same thing that

modern people mean when they say evolution. Use of these archaic terms is an attempt to convey the fact that people in the past had very different ideas about various kinds of changes in organisms—ideas that are difficult to understand and appreciate today. There was no solitary notion of 'evolution'. To write as if J.B. Lamarck, Erasmus Darwin, Geoffroy Saint-Hilaire, Robert Chambers, Darwin and Wallace, for example, all had 'the' idea of evolution is nonsense. Their ideas and theories often had almost nothing in common.

Weightings for historical evidence

In explaining myths in the history of science, historian Alberto Martinez stresses the responsibility qualified historians have to correct popular but historically inaccurate stories: ... if such corrective stories about myths are not clearly told and retold, the myths grow again, like tree branches in various directions' (Martinez 2011, p. 252). He provides a table of source credibility as used by historians but, unfortunately, rarely are such important principles explicitly laid out. First on his list of twenty is 'Original notes and drafts of the scientist's labors and ruminations'. The second to fourth also stress the high value of contemporary evidence in decreasing degrees of closeness to the events. His sixth is 'Early retrospective accounts by the scientist' whereas he gives later recollections the least value or reliability. An example is the famous Huxley–Wilberforce confrontation at Oxford in 1860, for which Frank James, Nanna Kaalund and other historians found that recollections of this event many years later were extremely unreliable (James 2005; Kaalund 2014).

CONCLUSION

Historians of science are not infallible nor immune from repeating, unwittingly, historically inaccurate stories about Wallace. They have repeated many of the claims discussed here no less than popular writers. This stems both from drawing on the published sources so widely available and the failure to analyse Wallace and scrutinise writings about him with the same rigour as has been the case with Darwin and other prominent figures from the history of science.

The prevalent themes of the modern Wallace story essentially reduce to two basic motifs. Firstly they exalt Wallace, and secondly they emphasise his disadvantages and victimhood in being unfairly treated and forgotten. If something said of Wallace (or any figure from the history of science) does either of these two things, one should be sceptical. Similarly, in too many cases anything proposed about Wallace that supports either motif has been accepted and repeated without question.

As for the difference in fame between Darwin and Wallace—both during their lifetimes and today—the answer is exceedingly simple. No one alive in the late 19th century would hesitate in explaining why one was a household name around the world and the other, although a respected one, never approached the former. Within about two decades of its publication Darwin's *Origin of Species* convinced the international scientific community and much of the literate public that evolution was a fact—a transformation of scientific understanding in which Wallace took almost no part, possibly not making any known converts to evolution in the 1860s–1870s when Darwin's book was most widely discussed and debated. It was because of the *Origin of Species* and later works, especially *The Descent of Man* (1871), that Darwin became, and has remained, so famous. It is no fault of Wallace that Darwin had started twenty years before him and published such unprecedentedly influential works.

Wallace was one of the great pioneers of the zoological exploration of Southeast Asia and proposed the single greatest zoogeographical distinction of the region, named in his honour as the Wallace Line by Huxley (1868). Wallace made countless contributions and discovered thousands of new species. In addition, his great work *The Malay Archipelago* (1869) remains one of the most interesting and delightful travel accounts of an early naturalist in the region, and continues to be read and to inspire new generations. No one can doubt that he deserves to be discussed and celebrated, but he also deserves to be accorded the highest standards of historical practice.

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Range of the greater bilby (*Macrotis lagotis*) in the Pilbara Region, Western Australia

MARTIN A. DZIMINSKI [1*], FIONA M. CARPENTER [1] & FRANK MORRIS [2]

[1] *Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, Government of Western Australia, Locked Bag 104, 6983 Bentley Delivery Centre, Western Australia, Australia*

[2] *PO Box 611, 6959 Fremantle Western Australia, Australia*

[*] *Corresponding author: ✉ martin.dziminski@dbca.wa.gov.au*

Abstract

Threatened greater bilby (*Macrotis lagotis*) populations in the Pilbara Region, where their distribution has been poorly documented, represent the extreme north-western extent of the species. We generated an accurate range of the bilby in this region from confirmed recent and historical records and identified areas of uncertain status. Their range covers approximately the eastern half, or 48%, of the Pilbara IBRA bioregion and 52% of the wider Pilbara Region (bioregion plus a buffer of 300 km). The western boundary of this range stretches south-east from approximately 50 km west of Port Hedland to about 350 km beyond Newman. Their range extends east and south-east into the Great Sandy, Little Sandy and Gibson Deserts, as well as northwards into the Kimberley. This study provides an accurate range for impact assessment and management decisions, and confirms the Pilbara Region as an important area for the persistence of wild bilby populations. Areas to the west and south-west of the confirmed range have unreliable or older records of bilbies and require further targeted surveys to confirm their absence in these areas.

Keywords: burrowing, critical weight range, occupancy, Matuwa, Lorna Glen, mammal, marsupial

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INTRODUCTION

The greater bilby (*Macrotis lagotis* Reid; hereafter referred to as the bilby), is an iconic burrowing marsupial in the Family Thylacomyidae and is of significant conservation and cultural value. It is an important ecosystem engineer (James & Eldridge 2007; Newell 2008; Read *et al.* 2008; James *et al.* 2011; Chapman 2013; Fleming *et al.* 2014; Hofstede & Dziminski 2017; Dawson *et al.* 2019) and an indicator species of environmental conditions (Southgate 1994). It is listed as 'vulnerable' under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999*, the Western Australian *Biodiversity Conservation Act 2016*, and by the International Union for the Conservation of Nature (2020). As well as having legislated protection, this species is important taxonomically, culturally to traditional owners (Paltridge 2016; Walsh & Custodians of the Bilby 2016) and is regarded as a national icon (Bradley *et al.* 2015). Once widespread across most of mainland Australia (Marlow 1958; Friend 1990; Gordon *et al.* 1990; Johnson & Southgate 1990; Southgate 1990a; Abbott 2001; Abbott 2008; Bradley *et al.* 2015), their range has contracted to approximately 20% of that prior to European settlement. The species is now found in the Pilbara, Kimberley and central deserts of Western Australia and the Northern Territory, and as an isolated population in south-western Queensland (Southgate 1990a; Bradley *et al.* 2015). Threats contributing to the species' decline include predation by feral cats and foxes (Paltridge 2002; Bradley *et al.* 2015) inappropriate fire regimes (Southgate & Carthew 2006; Southgate *et al.* 2007; Southgate & Carthew 2007; Bradley *et al.* 2015) and the degradation of habitat through pastoralism, introduced feral herbivores and clearing (Southgate 1990a; Pavey 2006; Bradley *et al.* 2015; Department of Environment 2016).

The Pilbara Region (Fig. 1) represents an important area for the continued survival of the most north-western wild populations (Cramer *et al.* 2017) given the contraction of the species from the remainder of the continent (Southgate 1990a; Bradley *et al.* 2015). Recent land clearing for agriculture and mining infrastructure (Brueckner *et al.* 2013) in the Pilbara may impact on bilbies, but there are only poorly constrained estimates of their range, which is otherwise undocumented in this region (e.g. Bradley *et al.* 2015). With the recent increase in development applications, and implementation of land management actions (Department of Water and Environmental Regulation 2020), an accurate range is needed to assist environmental impact assessment and management decisions at all levels of government in Australia. Of particular interest is the poorly documented western boundary.

The aim of this study was to generate an accurate range of the bilby within the Pilbara Region from confirmed recent and historical records and to identify areas of uncertain status within the region. Construction of a species distribution model (SDM) or mapping habitat suitability of the bilby in the Pilbara Region, which usually shows where a species may be found or where

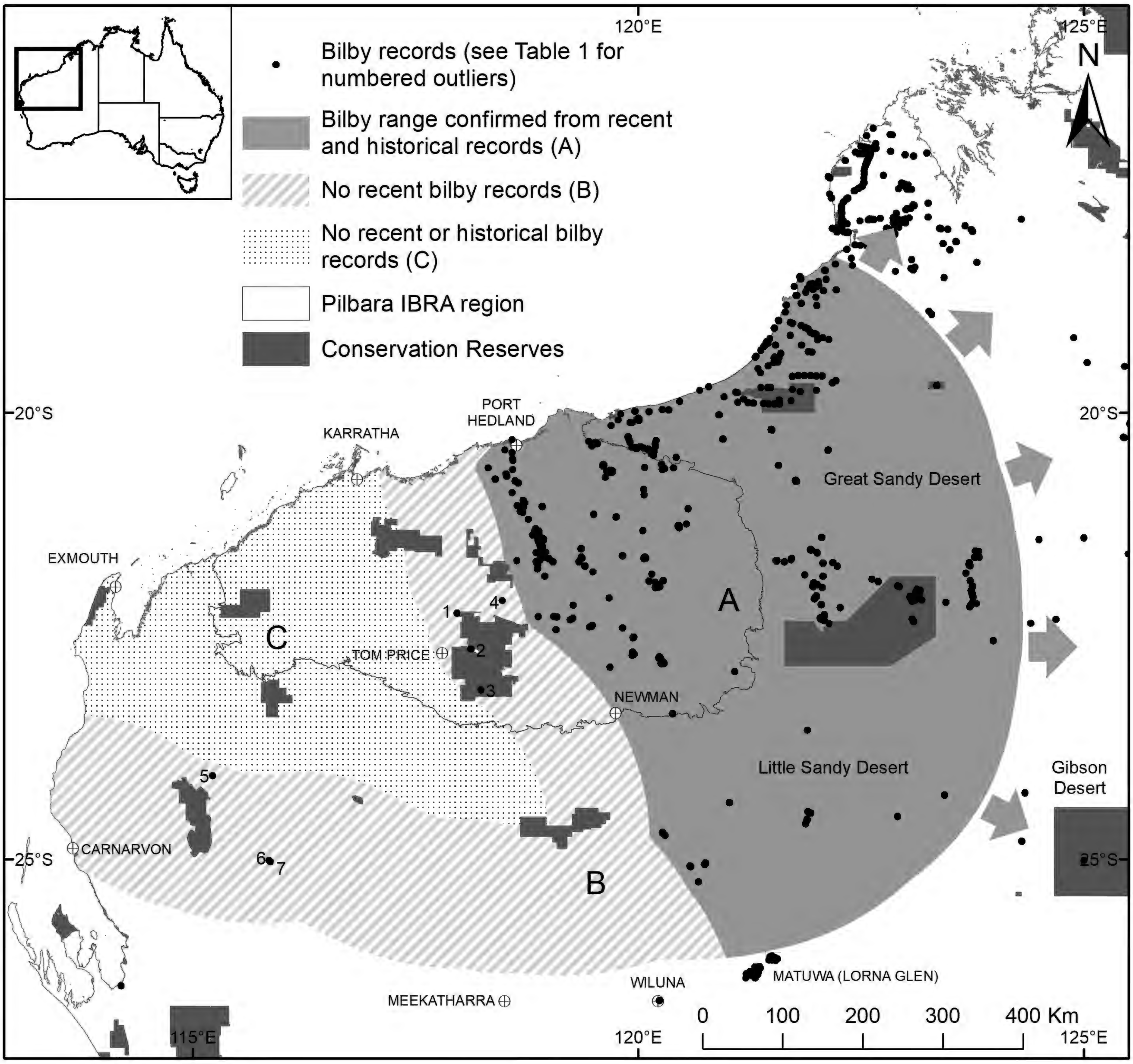

Figure 1. Bilby range in the Pilbara Region. Arrows indicate the bilby range continues into the southern Kimberley and central deserts.

there are suitable habitats for that species (Merow *et al.* 2013; Yackulic *et al.* 2013), will be the subject of future work.

METHODS

Bilby records were sourced from the Department of Biodiversity, Conservation and Attractions NatureMap database (NatureMap 2020), and the Pilbara Threatened Fauna Database. Records within the Pilbara Threatened Fauna Database were sourced from published and unpublished literature: the latter includes consultant and internal departmental survey reports covering areas within and surrounding the Pilbara, as well as liaison with departmental staff, consultants, mining companies, pastoral leaseholders and managers, and other land holders and users.

Records were screened for certainty and location accuracy. Uncertain records were discarded and only those with a location accuracy 10 km or less were included; however, we flagged any outliers from the main distribution of records for further examination even if they were uncertain or had low location accuracy. We generated a range employing a 300 km buffer surrounding the Pilbara bioregion (Thackway & Cresswell 1995; www.environment.gov.au/land/nrs/science/ibra accessed May 12, 2020)–this area is here referred to as the generalised 'Pilbara Region'. To delineate the range, we included all screened records in the analyses. Most records do not distinguish between observations of multiple bilbies or individuals as records of sign alone (e.g. scats, diggings, tracks, burrows, camera

Table 1. Key to numbered outlier bilby records from Figure 1.

No.	Year	Source	Observer	Description	Certainty	Accuracy
1	2001	Pilbara Threatened Fauna Database	Nearby pastoral lease holders	Saw possible bilby on road at the turn off to Hamersley Gorge 10 years ago (record taken 2/12/2011). Coordinates are of the location of the turn off road to Hamersley Gorge obtained from Google Earth as exact observation coordinates are unknown.	Uncertain	~200 m
2	1991	Pilbara Threatened Fauna Database	Ninox Wildlife Consulting (1992)	Evidence for their presence was based only on two burrows that may have been dug by bilbies. However, there has been no evidence of tracks, scats, or sightings (Environmental Protection Authority 1992).	Uncertain	~20 km
3	1984	Southgate (1990b)	Personnel involved in feral horse culling	O'brien's Well 1	Uncertain	~100 m
4	2001	Pilbara Threatened Fauna Database	Pastoral lease holders	Colony of bilbies were present at Mulga Downs 10 years ago (record taken 2/12/2011). Coordinates are indicative of Mulga Downs only (close to airport) and not representative of where the bilbies were. Note: several reliable records exist to the east on Mulga Downs Station, within the confirmed bilby range – it is most likely this record refers to that area.	Certain	~50 km
5	1969	NatureMap (2020)	Mr D. Evans	Day sighting. One only recently seen on station, apparently many in 1956, 1957 and 1958 (according to Mr J. A. Leeuven, Morley); Mr R. Ugle (station employee) stated that he had seen animals like that, also in Kennedy Ranges. ID confirmed with picture shown by investigating Warden.	Moderately certain	10 km
6	1969	NatureMap (2020)	-	Weedarra Station. Observed and ran off.	Moderately certain	10 km
7	1969	NatureMap (2020)	K. Teage	Weedarra Station. Five individuals observed that ran off.	Moderately certain	1 km

images) cannot determine the number of individuals. Each record is indicative of the confirmed presence of a bilby, or bilbies, at a specific time and location. We plotted all screened bilby records within 500 km of the Pilbara bioregion to ensure generated range boundaries at its edges were congruent with the extended bilby range. Conservation tenure was plotted to examine overlap with bilby range and distribution.

Three shapefiles were created, the first showing known bilby range and two other combined areas of potential and uncertain range. Outliers to the west of the main distribution of records were excluded to construct an alpha-concave hull using the 'alphahull' v2.2 package (Pateiro-Lopez & Rodriguez-Casal 2019) in R v3.6.2 (R Core Team 2020). A buffer of 15 km was added to account for populations that could shift up to 10 km over three years (Southgate & Possingham 1995) as well as the selected accuracy of 10 km to included records. It was then clipped with the Pilbara Region shapefile to represent a range from confirmed and accurate historical and recent records. Using the outliers near the western boundary of the known range (Fig. 1, points 1–4), the distance to the farthest of these outliers (plus a 15 km buffer) from the western boundary of the known range was used to create a polygon west of the main range. Similarly, the distance to the farthest of the south-western outliers (Fig. 1, points 5–7) from the southern boundary of the Pilbara Region (plus 15 km buffer) was used to create a polygon south-west of the main range. These two polygons were then merged to represent an area of uncertain range. All spatial analyses were completed using ArcGIS (Esri®) and QGIS software.

RESULTS

A total of 4386 bilby records, dating from 1899 to 2019, were included in the analysis (Fig. 2). These records have increased over the last 10 years due to surveys associated with expanded mining activities.

Within the Pilbara Region, the western boundary of the bilby range, established from recent and historical records, lies approximately 50 km west of Port Hedland and extends south-east beyond Newman (Fig. 1, area A). To the east and south-east there are no distinct boundaries to this range, which continues into the Great

Sandy, Little Sandy and Gibson Deserts, as well as into the south-western Kimberley. This confirmed bilby range represents 52% (34.4 million ha) of the Pilbara Region and 48% (8.5 million ha) of the Pilbara bioregion. In the Pilbara bioregion, there are no conservation reserves within the confirmed bilby range (Fig. 1).

To the west and south-west of the confirmed bilby range is an area of uncertain status (Fig. 1, area B). Within this area, there have been no extensive bilby surveys, and the only records present are either uncertain, have low location accuracy or were reported approximately 50 years ago (Table 1). In the area to the extreme north-west (Fig. 1, area C), there are no recent or historical bilby records, and no extensive bilby surveys.

DISCUSSION

Mapping the bilby range across the Pilbara Region based on positive, confirmed recent and historical records shows that their western extent is much farther west than previously estimated (Friend 1990; Southgate 1990a) and confirms previous attempts to map based on estimations without direct evidence of presence (Bradley *et al.* 2015). This increase in the known range across the Pilbara is due to the increased number of general fauna and targeted bilby surveys (Fig. 2). Furthermore, this increase may be attributed to more frequent recording of bilby signs (scats, tracks, burrows, diggings) rather than just captures or sightings, which make up the majority of historical records.

Bilbies are broadly distributed in the eastern half of the Pilbara Region and are linked to populations in the central deserts to the south-east and in the southern Kimberley to the north-east (Fig. 1). To the west and south-west of the confirmed bilby range is an area of uncertain status (Fig. 1, area B). The few records for this zone are either unreliable or old; however, bilby populations may be present. Terrestrial fauna surveys for environmental impact assessment are typically focused on species with a higher likelihood of being present in the area, and desktop assessments using existing and historical records. As the western portion of the Pilbara Region lacks records of bilbies, targeted surveys with definitive presence/absence records are not always incorporated in all surveys. Traditional surveys relied heavily on trapping of fauna, and because bilbies are not readily trapped (Southgate *et al.* 2019), it is possible that they have not been adequately surveyed across the Pilbara, particularly the areas designated as uncertain to the west and north-west in Figure 1.

In the extreme north-west of the Pilbara there have been no recent or historical bilby records (Fig. 1, area C). Consequently, the likelihood of populations being found in this region is low. Whereas there are several reasons for zero or few bilby records in the west of the Pilbara Region, existing minimal records do not necessarily indicate their absence. The two areas of uncertainty (Fig. 1, areas B and C) would benefit from widespread targeted bilby surveys (Cramer *et al.* 2017; Southgate *et al.* 2019), especially where there are suitable bilby habitats. Areas of habitat suitability can be derived from models (Hirzel *et al.* 2006), and focused on for future surveys to maximise efficiency.

Although some bilby populations exist on conservation reserves to the east (e.g. Walyarta Conservation Park, Karlamilyi National Park), bilbies are poorly protected by conservation reserves within the Pilbara bioregion. Within this bioregion their confirmed range encompasses 8.5 million ha (i.e. 48% of this region), but there are no conservation reserves in which bilby populations may be protected (Fig. 1). This may present complexities for future conservation management because most bilby populations are found on pastoral leases or mining tenements (Cramer *et al.* 2017).

This work also highlighted the importance of screening data as unscreened data can provide false, inflated or inaccurate distributions and ranges. For example, there are two excluded records from the

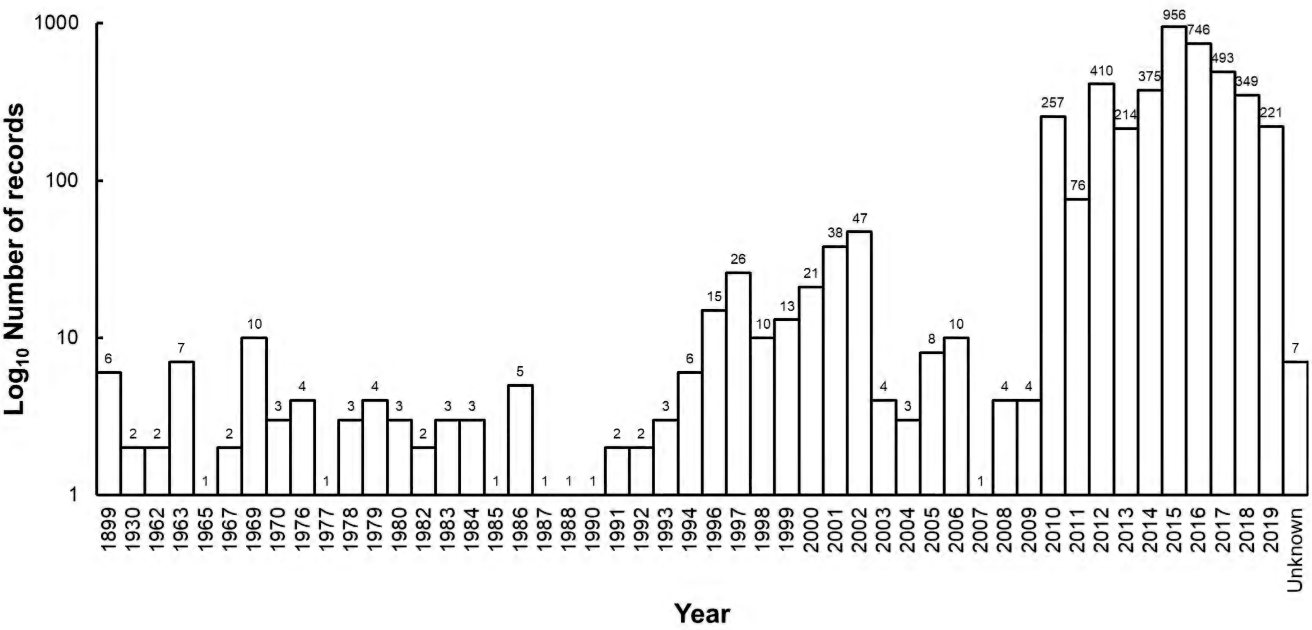

Figure 2. Frequency histogram of screened bilby records used in analyses (n = 4386).

1940s in which the distinguishing feature identifying the presence of bilby was the 'obnoxious smell of male' (NatureMap 2020). This is not a characteristic of bilbies and probably was confused with another species. Furthermore, sign data must also be carefully screened to avoid inclusion of misidentified observations (e.g. varanid lizard or rabbit diggings and burrows), and to ensure only verified evidence of bilbies is included (Southgate *et al.* 2019).

CONCLUSIONS

Our definition and mapping of bilby range across the Pilbara Region is based on reliable recent and historical records. This extent of occurrence represents 48% of the Pilbara bioregion and 52% of the wider Pilbara Region (bioregion plus a buffer of 300 km). To the west and south-west of this area targeted bilby surveys are required to confirm the absence of the species. The Pilbara Region includes the north-western edge of remaining wild bilby populations and confirms the area as important for the continued persistence of wild bilby populations, particularly as their range and occupancy reduces. This study provides both government and industry with an accurate range for informed, evidence-based, environmental impact assessment and management decisions. The bilby range shapefiles are available at the following link: https://www.rswa.org.au/publications/shape_files/2019_Pilbara_Bilby_Shapefiles.zip

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Rock pools (gnammas) in the Gibson Desert of Western Australia: unique formation and reasons for their limited biological diversity

BRIAN V. TIMMS [1*] & STUART HALSE [2]

[1] *Centre for Ecosystem Science, School of Biology, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2052.*

[2] *Bennelongia Pty Ltd, 5 Bishop Street, Jolimont. WA, 6014.*

* *Corresponding author: ✉ brian.timms@unsw.edu.au*

Abstract

Rock pools (gnammas) have a random distribution on rock pavements over much of Australia. In the climatically benign south, they are common and have a diverse fauna, but those in deserts are rarer, structurally different and scarcely surveyed. A widely spaced set of gnammas in the Gibson Desert of Western Australia were sampled in mid-2017 and again in mid-2018 using a pond net and a plankton net. The gnammas are in lateritic rock, and have a distinctive pipe-like form and mode of origin. The latter involves vertical solution of weathered rock, aided by kangaroos excavating for water as the pools dry. This is different from the granite pans and pits in southern Australia. Mean alpha diversity of macroinvertebrate communities in these mid-Western Australian gnammas is 5.9 species, drawn from a metacommunity of eight crustacean species, with perhaps a few insect individuals from an array of 21 species (gamma diversity). Invertebrate dispersal is extremely limited with crustaceans surviving dry periods as passively distributed eggs and insects recolonising actively from the wetter west during each filling event. Poor dispersal, plus the small size and homogeneity of habitat within the pipe gnammas, limits biotic diversity.

KEYWORDS: Geomorphology, diversity, dispersal, branchiopod crustaceans, aquatic insects.

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INTRODUCTION

Australia has a remarkable variety and number of inland rock pools formed largely by chemical corrosion. Usually they are known generically as ‘gnammas’, originally coined by the Noongar people of southwest Australia for pits in granite. These retain rainwater and once were an essential source of drinking water for human survival (Bayly 2011). Geologists and biologists in Australia have adopted the term for any rock pool, shallow or deep, formed by chemical corrosion in any rock type (including sandstone, limestone, quartzite, basalt, etc.) across Australia, each with characteristic geomorphology and processes of formation.

Although such landscape features have been variously recognised worldwide for centuries (e.g. Borlase 1769), the first substantive Australian work on their geomorphology dealt with granite outcrops on the northwestern Eyre Peninsula in South Australia (Twidale & Corbin 1963) and recognised pan gnammas, (shallow with flat floors) pit gnammas (deep, largely hemispherical bowls) and armchair gnammas (bevelled hollows in slopes). Recently Twidale & Bourne (2018) revised interpretation of processes in gnammas but omitted details of pit gnammas and did not refer to pipe gnammas in laterite in deserts (Bayly *et al*. 2011), which at the time were an inadequately described type of gnamma of the remote inland.

Detailed biological work on the pan gnammas of southwestern Australia (Bayly 1982, 1997; Pinder *et al.* 2000; Jocqué *et al.* 2007; Timms 2012a, b; Brendonck *et al.* 2015) recognised a distinctive fauna that Brendonck *et al*. (2016) considered the richest in the world for rock pools. Many faunal elements have special adaptations for living in shallow, crystal-clear waters with short seasonal hydroperiods (Brendonck *et al.* 2016). The deeper pit gnammas with longer hydroperiods and murkier waters support a largely different, far less diverse fauna with few special adaptations that is essentially a eurytopic fauna similar to that of any nearby freshwater pool (Timms 2014a). By contrast, the desert-pipe gnammas of Bayly *et al.* (2011) in the Victoria Desert of southeastern Western Australia apparently have a restricted eurytopic and depauperate fauna, which they explained by their extreme isolation and hence strong dispersal restrictions as well as the small size of the pools.

This paper aims to explore the geomorphology of pipe gnammas in the Gibson Desert of central inland Western Australia and provide an explanation for their formation. The second, more important, aim is to expand the biological database for inland pipe gnammas of Western Australian deserts to help explain their limited biological diversity. Biological collections were made from the Gibson Desert pipe gnammas during two periods with different rainfall conditions and from twice as many gnammas (or three times in a comparison of just pipe gnammas) as visited by Bayly *et al.* (2011).

STUDY AREA AND METHODS

Twenty-six rock holes adjacent to the Great Central Road between Laverton in Western Australia and the Northern Territory border to the east were visited twice in 2017–18 (Figs 1, 2; Appendix 1). The countryside is largely sandy with areas/ridges of lateritic rock and some exposed granite at Cosmo Newby. The area lies in the Canning and Officer basins, the Musgrove Province and on the edge of the Yilgarn Craton (Beard 2002; Appendix 1). The trip of July 1-4, 2017 followed 310.6 mm of rain during the previous six months (measured at Warburton, about midway along the transect; Fig. 1; Bureau of Meteorology 2018), so that all rock holes held water, and most were full (the wet trip). By contrast, during May 18–21, 2018 most of the pools were dry following low rainfall (33.8 mm) over the previous six months (the dry trip).

On the first visit to each pool, rock hollow depth was measured with a flexible steel tape and its average diameter determined by two measurements at right angles. Volumes were calculated using $V= \pi r^2 z$ where V = volume, r = average radius and z = depth. On the second trip it was noted that many of the holes were not quite vertical having been excavated by kangaroos searching for water. Whereas the depths of some holes changed by up to 5% due to these excavations, these changes were not added to the database. Conductivity was determined with an ADWA332 meter and turbidity was measured in a Secchi disc tube calibrated in Nephelometric Turbidity Units (NTU). This tube does not measure turbidity lower than 5 NTU so very clear waters were not accurately differentiated. If a pool was dry on the second trip a c. 500 g sample of bottom soil was taken from the upper 5 cm for later incubation to check on crustaceans likely to grow on wetting.

Where possible, zooplankton was collected with a small plankton net (opening 10 x 8 cm and 50 cm long, net mesh 159 µm) for one minute by swishing it around at various levels in the pools. Microfauna smaller than 160 µm, including rotifers, were not studied. Macroinvertebrates were caught with a 1 mm mesh pond net, 25 cm wide and 20 cm high with a 25 mm opening on a D frame. This net was swept through the pool three to four times for a total of no more than two minutes. Macroinvertebrates were sorted in a white tray, and representatives of all species caught were preserved in ethanol for later identification, with the remainder returned alive to the pools together with all tadpoles caught. All zooplankton collected was preserved in ethanol for later study. Though the study was not quantitative, relative abundances in the collections were estimated on a log scale (<10 = 0.1 to 0.9 depending on exact number; 10-99 = 1; 100-999 = 2; 1000-9999 = 3; >10000 = 4).

We used the correlation coefficient to test a possible relationship between gnamma size and alpha diversity, and a student's t-test to look for significant differences between two groups of gnammas (an east grouping of #1–10 and a west grouping of #14–23). The groups represent two distinct and geographically separate clusters of the randomly spaced gnammas along the transect (Fig. 1). Ten gnammas from each group were analysed to match the number in groups of other gnamma types in previous investigations (Timms 2012a, b; 2014a) and to eliminate differences due to unequal numbers involved. A Mantel test was used to test for autocorrelation between sites and their distance apart. To test questions of faunal relationships between these groups of gnammas, we used multivariate analyses with PRIMER (v5) (Clarke & Gorley 2001). We used

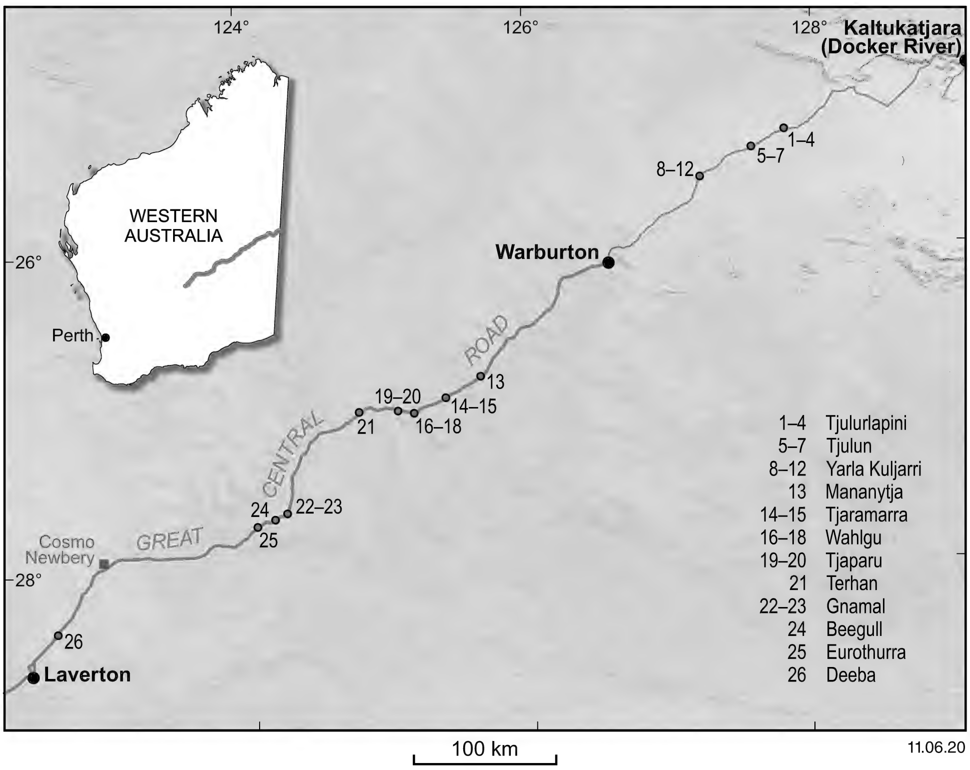

Figure 1. Location of the Great Central Road through the Gibson Desert showing the positions of studied gnammas.

Figure 2. Examples of pit gnammas: (a) Site 11, Karla Kuljarra, protected against camels by a Patjarr Spider; and (b) Site 15, Tjaramarra.

average abundance values collected over many visits to the Wheatbelt localities, whereas abundances for all the Gibson sites are from the 2017 field trip. Otherwise, the collecting and analyses protocols for all the data are similar. Field and laboratory counts were log-transformed ($\log_{10}(x+1)$) and a similarity matrix was constructed using the Bray-Curtis similarity coefficient. Non-metric multidimensional scaling (nMDS) ordination was then performed to visualise patterns in assemblage composition among the data sets. One-way analysis of similarities (ANOSIM) was then used to test significance of the differences. In these ANOSIMs, the magnitude of the associated R statistic value was used as an absolute measure of difference between paired groups. In general, if R > 0.75, groups are clearly distinguishable, if R > 0.5, groups overlap but are clearly different, and if R < 0.25, groups are typically indistinguishable (Clarke & Gorley 2001). Finally, similarity percentage analysis was performed to determine the species characteristic of each for four major groups identified in the nMDS (the Gibson pipes, the Wheatbelt pits and two groups of the Wheatbelt pans) and those that distinguish between these major groups (Clarke 1993).

RESULTS

Of the 26 gnammas studied in the Gibson Desert, the mean depth was 116.8 cm, mean diameter 130.4 cm and mean volume when full was 2.09 m^3 (Table 1). These figures hide considerable variation, so that extreme depths combined with extreme volumes cause the volumes to be the most variable parameter (Table 1). Whereas the typical shape is a wide vertical pipe, many gnammas have outward sloping walls at least on one side, where kangaroos actively dig as the pool approaches dryness. Unfortunately, pools closest to the road often contained bottles, tin cans, car parts and ad hoc depth sticks. Some had cobbles, the most notable being Beegull, which is not a pipe gnamma as are all the others but a plunge pool along a waterway. The Cosmo Newbury area was also different by having granite outcrops, but there were no pit gnammas (sensu Timms 2013a) presently deep enough for study, all being almost, if not entirely, full of sediment.

Water was always fresh and pools were either almost clear or somewhat turbid, i.e. values had a bimodal distribution, explained in many cases by catchments of either bare rock or exposed soil. Electrical conductivity and turbidity values were higher in the dry trip, though data were scant on the second trip (Table 1). These values are indicative only, as they undoubtedly vary with stage of filling and seasonal productivity/turbid inflows (Timms 2017).

Alpha diversity (i.e. momentary species richness) of macroinvertebrates in the pools averaged 5.9 with 3.3 crustacean species and 2.6 insects per pool, with the later more variable than the former (Tables 1, 2). Alpha diversity was unrelated to pool depth, pool volume or pool clumping, except for insect diversity, which is related to pool volume ($r = 0.502$, $P < 0.01$). Crustacean individuals were always more numerous than insect individuals (crustaceans 10 to >10000 per collection, usually >1000, while insects were generally < 100 for dipterans and <10 for others, often just 1–2). Overall, eight species of crustaceans and 21 insect species were encountered—the additional insect species found in the dry year of 2018 are accounted for in Table 2. The most common crustaceans were the ostracods *Sarscypridopsis* nr *aculeata* and *Heterocypris* n.sp. BOS1137, and the laevicaudatan *Lynceus baylyi*, whereas the dominant insects were *Chironomus* spp. and the beetles *Sternopriscus multumaculatus* and *Eretes australis* (Table 2). Rehydration of muds collected on the 2018 trip did not add to crustacean diversity (Table 2), but largely confirmed existing distributions, with the exception of *Mesocyclops brooksi,* which was not observed in any culture.

Distribution of species is patchy. Among the crustaceans, *Lynceus baylyi* is absent from the Tjulun group, *Daphnia carinata* is absent from gnammas east of Wahlgu and *Moina australiensis* so far has not been found west of the Yarla Kuljara group (Table 2). Insect distribution is even more random, though the more common species appear somewhat regularly throughout the study area (Table 2). We found no evidence of spatial autocorrelation from a Mantel test (p=0.976, 9999 permutations). However, by a t-test, which assumes independence among samples, insects were significantly different ($t = 0.0362$, $P < 0.05$) between the east pools (#1–10, n=1.5 species per pool) and the west

pools (#14–23, n=3.0 species per pool) where mean pool volumes were similar (t = 0.4744, P> 0.05).

DISCUSSION

The pipe gnammas of the western deserts have a distinctive geomorphology, with a wide near vertical pipe averaging 110 cm deep and 130 cm diameter (Bayly *et al*. 2011; Table 1, Appendix 1). These gnammas have formed in laterite, seemingly by long-term dissolution of the cementing chemicals binding the rock. Once a surface depression forms, a pipe can develop as solution is largely vertical from the overlying pooled water. The side walls are rough with harder remnants of the lateritic conglomerate rock protruding. At many sites, deepening is promoted by excavation by kangaroos. In the past, Aboriginal people may have removed sediment to create larger water storages to aid survival.

Similar gnammas, called native wells, are known in lateritic rocks in central western Queensland (e.g. near Jundah, Windorah; BV Timms, unpublished data). All these pipe gnammas are distinctive and different from the pit gnammas on granite, which generally are pudding-basin shaped or canoe-shaped (Timms 2014a, b; Twidale & Corbin 1963; Twidale & Bourne 2018). The most similar pit gnammas are some vertical cylinders, partly cut by surface water descending to a void below (Twidale & Bourne 2018)—their walls are smooth and with no animal activity involved in their formation.

Water in the desert pipe gnammas is always fresh, though with a minor increase in salts due to evaporation. It is rare for gnamma waters across Australia to be hyposaline, the exception being a few western Nullarbor granitic pools (Timms 2012b). Water clarity is generally in the same range as for pit gnammas (Timms 2014a, b) and for most not quite as crystal clear as in pan gnammas. Clarity decreases as the pools dry, but algae blooms colouring them green were not observed in the desert as in some pit gnammas in agricultural areas to the southwest (Timms 2014a).

For crustaceans, there is strong concordance between the results obtained by Bayly *et al*. (2011) for eight pipe gnammas in the Great Victoria Desert and the present results for the Gibson Desert; for both studies *Lynceus baylyi* (*Lynceus* sp. nov. in Bayly *et al*. 2011), *Moina australiensis, Sarscypridopsis* and *Heterocypris* were important taxa. *Daphnia* was not recorded in the former study and neither were Hemiptera or Coleoptera. These differences could be sampling anomalies due to fewer sites sampled in the Victoria Desert, or lower diversity due to lower mean annual rainfall (Gentilli 1986) imposing shorted hydroperiods (Brendonck *et al*. 2015) or poorer dispersal due to greater spatial distribution of gnammas there (Vanschoenwinkel *et al*. 2008a).

At an alpha diversity of 5.9 in the Gibson pipe gnammas (Table 1) and 4.6 in those in the Victoria Desert (Bayly *et al*. 2011), the faunas of these desert pipe gnammas are depauperate compared to almost all groups of gnammas so far studied in Australia. Pit gnammas on Yilgarn granite to their southeast averaged 8.2 and those on Eyre Peninsula, South Australia, averaged 9.1 species (Timms 2014b). Pan gnamma faunas are usually much more diverse, with an alpha diversity of about 30 species per pan in the Western Australian Wheatbelt (Timms 2012a), and lower (8.1 - 9.7) in eastern Australia (Timms 2012a, 2014a, 2017). The exception is Stanthorpe, Queensland, at 5.6 species in its much shallower pan gnammas (Timms *et al*. 2019). These pan gnamma species are part of a metacommunity, with figures per rock outcrop and district much higher than for individual pans—the latter reaching at least 220 in southwest Australia (Pinder *et al*. 2000). These figures do not include microfauna, which generally are a minor component—rotifers averaging just four species per pool in nine groups of rock pools in Western Australia (Pinder *et al.* 2000).

Comparative figures for the metacommunities of the deeper gnammas are even more instructive. Gibson Desert pipes appear to support a more diverse community than the Victoria Desert pipes (29 vs 14 species; Bayly *et al*. 2011), although three times as many pipes were examined in the Gibson Desert and insects were identified to genus or species level rather than to family level as in the Victoria Desert study. The limited fauna of desert pipes in both areas is obvious in comparison with the pits of the wetter Yilgarn region of Western Australia, where the metacommunity totals 82 taxa (Timms 2014) compared to about 35 overall in the desert pipes (this study, plus Bayly *et al*. 2011).

Table 1. Various parameters of the gnammas with year assessed.

Parameter	n	Mean ± SD	Range
Geomorphology (2017)	26	Depth 116.8 ± 31.1 cm Diameter 130.4 ± 63.8 cm Volume 2.09 ± 2.42 m^3	37–170 cm 70–275 cm 0.06 – 8.12 m^3
Physicochemical features (2017)	26	Conductivity 117 ± 199 μS/cm Turbidity 18.8 ± 17.8 NTU	97–463 μS/cm 5–32 NTU
Physiochemical features (2018)	4	Conductivity 448 ± 410 μS/cm Turbidity 60.0 ± 68.5 NTU	221–1282 uS/cm 5–150 NTU
Species richness (2017)	26	Crustaceans 3.27 ± 1.31 Insects 2.58 ± 2.35	0–5 2–11
Species richness (2018)	4	Crustaceans 0.25 Insects 2.25	0–1 1–6

Table 2. Species list for the Gibson gnammas

Crustacea	Records	2017*	2018*^
Lynceus baylyi	15	1, 3, 10–12, 14–17, 19–21, 24–26	*1, 2, 9–11, 14, 17, 19–21, 24*
Daphnia carinata s.l.	8	2–5,8,10,11,14,15	*2–6, 8–11, 14*
Moina australiensis	6	14–18, 25	*14–15*
Heterocypris n. sp. BOS1136	1	24	
Heterocypris n. sp. BOS1137	18	1–3, 8, 10–24	*1–4, 8–10, 14–15, 18–22, 24*
Ilyodromus ? viridulus	1	24	
Sarscypridopsis nr *aculeata*	23	1–4, 6–9, 11–26	*1–3, 6–12, 18–20, 24–25*
Mesocyclops brooksi	7	1, 2, 8, 9, 12, 21, 26	
Insecta			
Hemicordulia tau	1	26	
Micronecta sp.	1		26
Anisops gratis	1	1	
Anisops hyperion	6	1, 7, 15, 20, 21, 24	
Anisops stali	9	6, 7, 15, 19–21, 23, 24	26
Anisops thienemanni	3	15, 24, 26	
Agraptoocrixa hirsuta	2	1, 15,	
Agraptocoruxa parvipunctata	4	21, 24, 26	26
Antiporus gilberti	1		26
Enochrus sp.	1	24	
Eretes australis	7	1, 6, 7, 13, 21, 23, 24	16–17, 23
Hyphydrus elegans	1	26	
Necterosoma sp.	1	26	
Sternopriscus multimaculatus	13	2, 4, 7, 11, 12, 14, 16, 18–21, 24	26
unidentified tanypodine	1	26	
Chironomus alternans	10	8–12, 14–15, 19, 21, 24	26
Chironomus australis	3	15, 16, 18	
Chironomus tepperi	4	15, 19, 21, 24	
Dasyhelea sp.	1	17	
Cryptochironomus sp.	4	20–22, 24	
Culex australicus	4	9, 13, 14, 23	
Arachnida			
Mite	2	10, 24	

* individual gnammas referred to by their numbers given in Figure 1

^ cultured crustaceans in italics; extant insects collected in 2018.

Much of the invertebrate fauna of the desert pipe gnammas is a limited subset of that in Yilgarn pit gnammas, although the only laevicaudatan present in the desert pipes is distinctive; *Lynceus baylyi* is almost entirely restricted to desert gnammas compared to the common *Lynceus magdaleanae* of the Yilgarn pits (Timms 2013b). Cladocerans are the same at the alpha species level (*Daphnia carinata* sensu lato and *Moina australiensis*) whereas among the ostracods there is uncertainty due to taxonomic limitations—genera are shared but there may be differences among the species present. As for the pits, there is a vast difference in community composition between the desert pipes and Yilgarn/Pilbara pan gnammas. The pans have a variety of branchiopods, cladocerans, ostracods, copepods, and a wider range of insects (Bayly 1982, 1997; Pinder *et al*. 2000; Jocque *et al*. 2007; Timms 2012a, b).

Ordination of the pipe gnammas with pit and pan gnammas in southern Western Australia reveals the pipes have a community structure separate from that of both pit gnammas and pan gnammas in other parts of the state (Fig. 3). Both Gibson groups cluster near the lower right-hand corner, the four groups of pit gnammas are also to the right, whereas the pans form a cluster, in two groups, to the left. Three of the four major groups are significantly different from one other (i.e. $R > 0.75$) and even the southeastern pans are largely different (R between 0.5 and 0.75) from the northern pans (Table 3). The species most typical of the four groups are (a) *Sarscypridopsis* nr *aculeata*, *Lynceus baylyi,* and *Heterocypris* sp. for the Gibson pipes; (b): *Chironomus tepperi, Cypridopsis* sp., and *Sternopriscus multimaculatus* for the Wheatbelt pits; (c) *Boeckella longirostris, Amphibolis* sp., and *Paralimnadia badia* from the northwest pans; and (d) *Boeckella opaqua, Pleurispina* sp., and *Ceriodaphnia* sp. in the southeast pans.

As Bayly *et al*. (2011) noted, the fauna in these desert pools is severely restricted by ineffective dispersal, particularly as it is hindered by the small surface area of water available to receive dispersants among vast areas of sand and rock—this is especially so for insects which must colonise each filling. In addition, the habitat is relatively homogeneous within the pipes and macroscopic plants are almost entirely absent. The one Victoria Desert pool with macrophytes had an extra three cladocerans and an ostracod (Bayly *et al*. 2011).

It is likely that limitations on dispersal ability are responsible for the patchy distribution of many species in the Gibson Desert (Table 2). Branchiopod

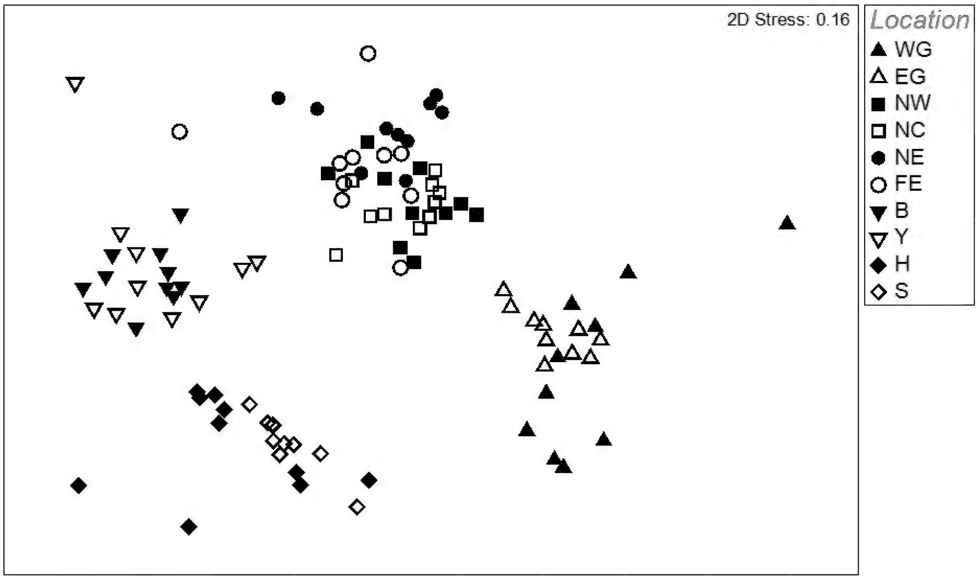

Figure 3. Ordination diagram of two groups of 10 each of Gibson pipe gnammas (EG = #1–10; WG = #13–22) with 4 groups of 10 each of pit gnammas in the northern and eastern Wheatbelt on Yilgarn granite of Western Australia and 4 groups of similiarly located pan gnammas. Data for gnammas other than the pipes from Timms (2012a, b, 2014a). Pit gnammas: NW = near Beacon, NC = near Trayning; NE near Yanneymooning; FE = near Hyden. Pan gnammas: B = near Paynes Find; Y = near Yanneymooning; H = near Hyden; S = near Norseman.

Table 3. ANOSIM statistic R for pairwise tests between G = Pipe gnamma sites in Gibson desert, W = pit gnamma sites in Wheatbelt, N = pan gnamma sites in northern Wheatbelt and S = southeastern sites in Wheatbelt.

Pairwise tests	R statistic
G, W	0.845
G, N	0.950
G, S	0.905
W, N	0.914
W, S	0.947
N, S	0.619

crustaceans are often dispersed by waterbirds and/or wind (Vanschoenwinkel *et al*. 2008a; Rogers 2014), but with no water birds observed during field trips and with the orifice of the pipes being extremely small, and so catching little dust, dispersal opportunities for crustaceans are particularly poor in the Gibson Desert. Mammals are also known to disperse eggs on occasions (Vanschoenwinkel *et al*. 2008b, 2011) and it is possible kangaroos may infrequently disperse small eggs via their fur. Insect distribution is particularly patchy (Table 2) because new colonization is needed after each refill, and few hemipteran and coleopteran individuals are successful in finding pipes, making the process even more disordered. The greater abundance of insects in western pools suggest colonization is from the west under the influence of the dominant westerly winds and the more numerous wetlands to the west, e.g. Laverton wetlands. For dipterans, adults apparently persist around only a few pools when they dry and nearly all recolonization is restricted to these pools. For example, mosquitoes rarely, if ever, are found at pools hundreds of kilometres from source wetlands (Service 1997). This inefficient dispersal is reflected in the limited correlation between pool size and diversity, a feature of the pit gnammas of the Yilgarn granites (Timms 2014a).

Davis *et al*. (2018) show that latitude is a driver in diversity in various habitats across the arid biome, including rock pools. However, they fail to note the fundamental difference between shallow pan and deeper pit/pipe-gnamma communities (see above). It is thus invalid to compare Pilbara pans with Victoria Desert pipe gnammas as only similar geomorphic units should be compared. When this is done there is still a decrease of diversity with some increase in latitude if, for instance, the Pilbara pan at 20° 44′S (with an alpha diversity of 18.5; Pinder *et al*. 2010) is compared with structurally similar Walga Rock pans at 27° 24′S (alpha diversity 10.6; Timms 2012a). However, even this difference is misleading as the reduction in alpha diversity is due principally to different hydrologies (Brendonck *et al*. 2011) and not, in the first instance, to latitude.

CONCLUSIONS

The wide pipe-like morphology of pipe gnammas, with kangaroos contributing to their enlargement, makes them unique. By comparison with other gnammas, invertebrate diversity is particularly low with mean species richness of only 5.9 per pool. The laevicaudatan *Lynceus baylyi* and undescribed species of *Heterocypris* and *Sarscypridopsis* nr *aculeata* ostracods dominate among the crustsceans, but among insects there is an array of hemipterans, coleopterans and dipterans with *Sternopriscus multumaculatus* and *Chironomus* spp. the most widespread. There are severe limitations on dispersal of all species.

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APPENDIX

Table 1. Location and physical characterics of the gnammas along the Great Central Road.

number	Name	Coordinates	total depth (cm)	diameter (cm)	volume (m^3)	Species Richness Crustaceans	Insects	Total
1	Tjulurlapini 1 (N)	25°18'00.54"S, 127°49'02.16"E	100	110	0.95	4	3	7
2	Tjulurlapini 2 (middle)	25°18'00.54"S, 127°49'02.28"E	105	113	1.05	4	1	5
3	Tjulurlapini 3 (middle)	25°18'00.84"S, 127°49'02.28"E	72	85	0.41	5	0	5
4	Tjulurlapini 4 (SW)	25°18'00.66"S, 127°49'01.92"E	142	255	7.25	3	1	4
5	Tjulun 1 (N)	25°24'42.78"S, 127°35'11.46"E	37	118	0.40	1	0	1
6	Tjulun 2 (middle)	25°24'43.08"S, 127°35'11.04"E	144	268	8.12	1	2	3
7	Tjulun 3 (S)	25°24'43.14"S, 127°35'10.86"E	93	103	0.77	0	2	2
8	Yarla Kuljarri 1 (N)	25°35'50.82"S, 127°13'31.56"E	150	90	0.95	5	2	7
9	Yarla Kuljarri 2 (middle)	25°35'51.36"E, 127°13'31.14"E	112	70	0.43	3	2	5
10	Yarla Kulgarri 4 (middle)	25°35'51.42"S, 127°13'31.20"E	118	73	0.49	4	2	6
11	Yarla Kuljarri 6 (S)	25°35'51.42"S, 127°13'31.26"E	40	78	0.06	4	2	6
12	Yarla Kuljarri 9 (SW)	25°35'51.96"S, 127°13'31.50"E	132	128	1.70	4	2	6
13	Mananytja	26°50'12.66"S, 125°39'37.02"E	130	73	0.54	2	1	3
14	Tjaramarra N	26°50'02.94"S, 125°24'44.28"E	105	185	2.82	3	2	5
15	Tjaramarra S	26°50'08.46"S, 125°24'39.24"E	128	173	3.01	5	6	11
16	Wahlgu N	27°03'37.56"S, 125°11'07.56"E	170	98	1.28	4	1	5
17	Wahlgu W	27°03'38.16"S, 125°11'05.82"E	110	108	1.01	4	1	5
18	Wahlgu SE	27°03'38.34"S, 125°11'06.90"E	120	130	1.59	3	3	6
19	Tjaparu N	27°02'35.52"S, 125°04'12.36"E	148	102	1.21	3	5	8
20	Tjaparu S	27°02'35.58"S, 125°04'12.42"E	105	90	0.67	4	2	6
21	Terhan	27°02'39.18"S, 124°47'47.28"E	125	275	7.42	4	7	11
22	Gnamal NE	27°40'06.30"S, 124°15'47.34"E	115	62	0.35	4	1	5
23	Gnamal SW	27°40'06.84"S, 124°15'48.00"E	125	85	0.71	1	2	3
24	Beegull	27°42'19.56"S, 124°10'34.20"E	125	242	6.74	4	10	14
25	Eurothurra	27°44'45.78"S, 124°02'57.18"E	152	132	2.08	3	1	4
26	Deeba	28°22'06.66"S, 122°35'43.38"E	135	145	2.23	3	6	9
means			116.8	130.4	2.09	3.27	2.58	5.85

Cluster roots are common in *Daviesia* and allies (Mirbelioids; Fabaceae)

FRANCIS J. NGE [1, 2], MARION L. CAMBRIDGE [3, 4], DAVID S. ELLSWORTH [5], HONGTAO ZHONG [3] & HANS LAMBERS [3 *]

[1] *School of Biological Sciences, Faculty of Science, The University of Adelaide, Adelaide, SA, Australia 5005, Australia*

[2] *State Herbarium of South Australia, PO Box 1047, Adelaide, SA 5001, Australia*

[3] *School of Biological Sciences, The University of Western Australia, Crawley, WA 6009, Australia*

[4] *Oceans Institute, The University of Western Australia, Crawley, WA 6009, Australia*

[5] *Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2751, Australia*

* *Corresponding author:* ✉ *hans.lambers@uwa.edu.au*

Abstract

Cluster roots are best known in the Proteaceae, but also occur in other plant families. Cluster roots are produced by *Viminaria juncea* and some species of *Daviesia*, which belong to the Australian Mirbelioids (Fabaceae). We searched for cluster roots in a number of species in *Daviesia* and its close allies *Gompholobium* and *Sphaerolobium* and found them in all studied species of these three genera. *Daviesia incrassata* subsp. *incrassata*, collected at an unusually waterlogged habitat, had no cluster roots, but they were present in *D. incrassata* subsp. *reversifolia* in a drier habitat. Cluster roots are pervasive in the *Daviesia* group of the Fabaceae, allowing them to persist on low-phosphorus soils.

Keywords: Australia, cluster roots, *Daviesia*, Fabaceae, *Gompholobium*, low-nutrient soils, Proteaceae, *Sphaerolobium*

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INTRODUCTION

Fabaceae are considered a mycorrhizal family (Wang & Qiu 2006), but there are several examples of non-mycorrhizal genera in this family, most prominently *Lupinus* (Vierheilig *et al.* 1994; Treu *et al.* 1995; Trinick 1977; Oba *et al.* 2001). Other species have cluster roots, or both cluster and mycorrhizal roots; for example, some non-mycorrhizal species of *Lupinus* native to the Mediterranean region produce cluster roots (Lambers *et al.* 2013), and the South African fabaceous *Aspalathus linearis* is mycorrhizal and also produces cluster roots (Hawkins *et al.* 2011).

Among Australian Fabaceae, *Viminaria juncea* has long been known to be both mycorrhizal and to produce cluster roots (Lamont 1972; Brundrett & Abbott 1991), whereas *Daviesia cordata* and *D. decurrens* produce cluster roots but are non-mycorrhizal (Brundrett & Abbott 1991; de Campos et al. 2013). *Daviesia physodes* also produces cluster roots, but its mycorrhizal status has not been evaluated (Lambers *et al.* 2019). *Daviesia reclinata* in northern Australia has arbuscular mycorrhizal roots (Brundrett 2017). These taxa belong to the Mirbelioids (Papilionoid tribes Mirbelieae and Bossieeae; Table 1), which contain many species-rich Australian sclerophyllous genera (Crisp & Cook 2003a). *Daviesia* species are scleromorphic shrubs endemic to Australia (Fig. 1a), where they comprise the largest genus of Fabaceae subfamily Papilionoideae, with 131 species (Crisp *et al.* 2017). The genus is distributed across Australia in all major habitats, except wetlands and rainforests. Early suggestions that another Australian pea genus (*Kennedia*) in another tribe (Phaseoleae; Papilionoideae; Table 1) might produce cluster roots (Adams *et al.* 2002) were not substantiated when this was followed up in a detailed survey of carboxylate release from roots of several mycorrhizal and non-mycorrhizal species of *Kennedia* (Ryan *et al*. 2012; Suriyagoda *et al.* 2012.

Viminaria (Fig. 1d) and *Daviesia* belong to the large antipodal group of Mirbelioids, or the *Daviesia* group *sensu* Crisp & Cook (2003b) and a few species have cluster roots. Our aim was first, to discover whether cluster roots are present in additional species of *Daviesia* and, second, whether they are also present in other Mirbelioid genera (Table 1), such as *Gompholobium* (Fig. 1b) and *Sphaerolobium* (Fig. 1c; Crisp & Cook 2003a). Determining whether other species within the group produce cluster roots may give insight into their evolutionary history, and how these species are able to colonise and persist on

Table 1. Formal and informal infrageneric classification of *Daviesia* and allies in Fabaceae mentioned in this study.

Subfamily	Tribe	Group	Genera
Papilionoideae	Mirbelieae and Bossieae (not limited to taxa from '*Daviesia* group')	Mirbelioids or '*Daviesia* group' sensu Crisp & Cook (2003b)	*Daviesia* *Erichsenia* *Gompholobium* *Sphaerolobium* *Viminaria*
	Phaseoleae	n/a	*Kennedia*

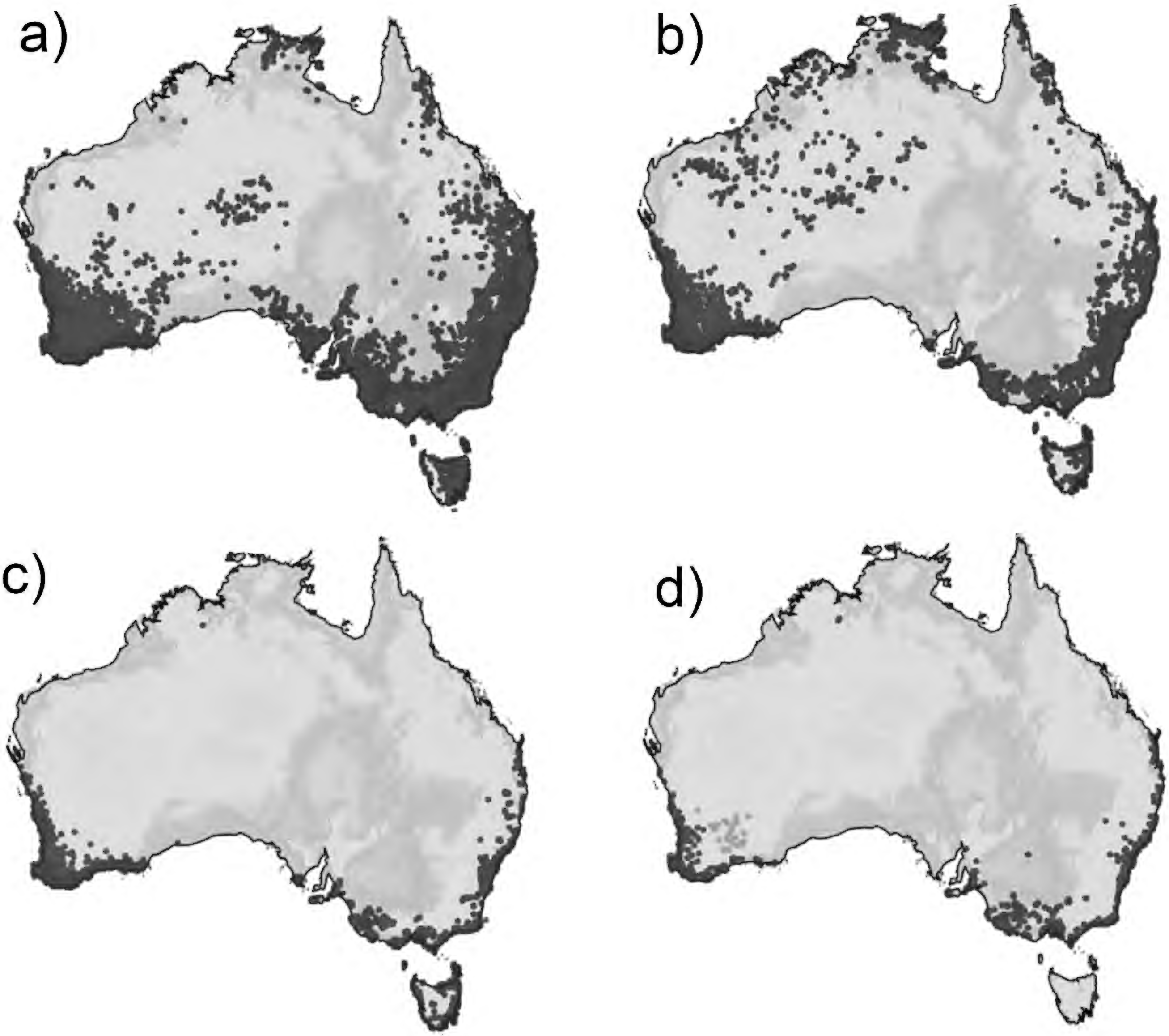

Figure 1. Distributional range of a) *Daviesia,* b) *Gompholobium,* c) *Sphaerolobium,* d) *Viminaria* (blue) and *Erichsenia* (red), sourced from collection records from the Australasian Virtual Herbarium. Map of Australia shaded by topographic contours (orange–high elevation; blue–low elevation) sourced from the spatial portal of Atlas of Living Australia. Details of locations of sampled species are included in Table 2.

low-nutrient, sandy soils, particularly if phosphorus (P) is relatively unavailable. Evidence of how common cluster roots are in this distinct evolutionary lineage within Fabaceae may then give an indication of the importance of this trait.

MATERIALS AND METHODS

We concentrated on sampling sites in southwest Western Australia as most of the *Daviesia* species are found in that region, but we also included sites in South Australia, Victoria and New South Wales (Fig. 2).

Roots of Fabaceae in the *Daviesia* group were collected close to their main stem, making sure to trace them back to the individual stem, to avoid confusion with cluster roots belonging to adjacent species (Abrahão *et al.* 2018). We identified cluster roots on the basis of their distinctive morphology (Shane & Lambers 2005). Purnell (1960) described cluster roots in Proteaceae, as dense clusters of rootlets of limited growth. She referred to each cluster of rootlets as a 'proteoid root' and to that section of the lateral root from which the rootlets arise as the 'axis of the proteoid root'. As these roots have since been found in a range of other families, the term proteoid root has gradually been replaced by 'cluster root' (Shane & Lambers 2005).

RESULTS

We found cluster roots in a wide range of species in the *Daviesia* group at several locations in Western Australia, South Australia, Victoria and New South Wales, and

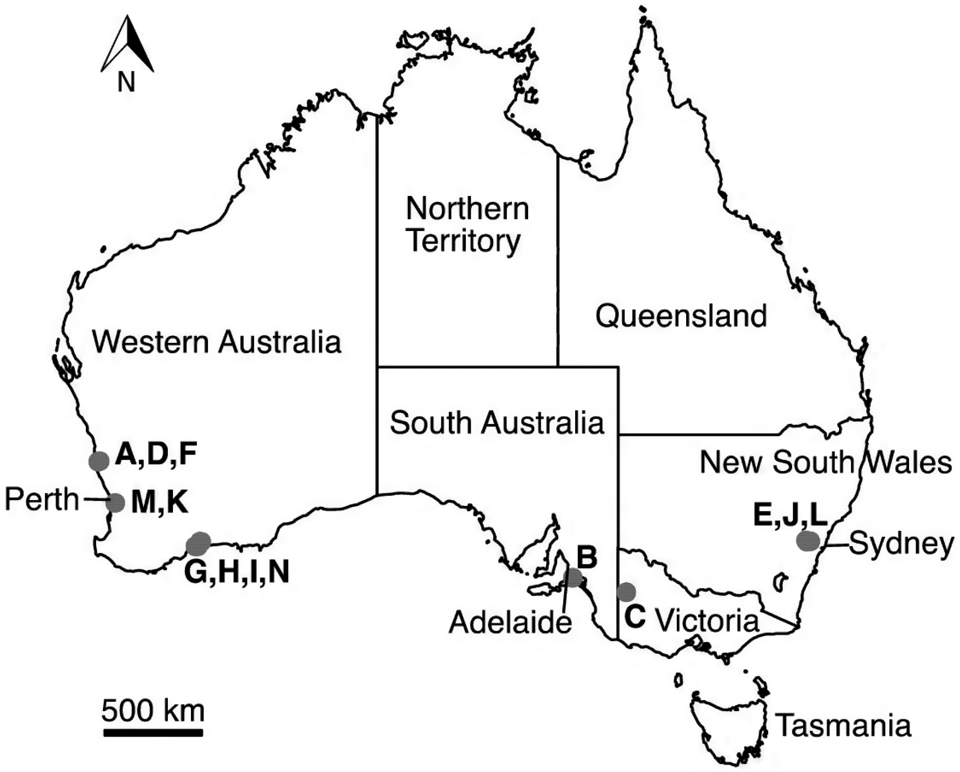

Figure 2. Sampling location of the species sampled in this study – denoted with red dots. The letters on the map refer to the species listed in Table 2.

present evidence for cluster roots in an additional 12 species within the genus (Table 2, Figs 3, 4). Furthermore, *Daviesia* species with cluster roots are scattered across the species level phylogeny from Crisp *et al.* (2017), suggesting that this trait is not clade-specific and most likely common across the genus (Fig. 5). We also document cluster roots in two additional genera within Mirbelioids, – *Gompholobium* and *Sphaerolobium* (Table 2, Fig. 4f).

DISCUSSION

Prior to this study, only two genera in the *Daviesia* group (Mirbelieae), namely *Viminaria* (Lamont 1972; Walker *et al.* 1983) and *Daviesia* (Lambers *et al.* 2019; Brundrett & Abbott 1991), were known to produce cluster roots. We discovered that cluster roots were present in 12 new species of *Daviesia,* and in two additional genera, *Gompholobium* and *Sphaerolobium*. Cluster roots were present in *Daviesia* species across all of our sampling sites except for one waterlogged site. This is significant, because it suggests the trait might be common across all *Daviesia* species, and hence is likely important to the ecology of the genus and its allies. In addition, within *Daviesia* this trait is not clade-specific, with documented species that possess cluster roots scattered across the species-level phylogeny (Fig. 5), again indicating that the trait is likely common across the genus.

Pate *et al.* (1989) noted anomalous secondary thickening in roots of *Daviesia*, which Crisp & Cook (2003b) subsequently referred to as 'cord roots'. No function has been proposed for cord roots (Pate & Dixon 1996). None of these authors mentioned cluster roots for this genus, although they had been firmly established in the *Daviesia* group, first in *Viminaria juncea* (Lamont 1972; Walker *et al.* 1983) and later in two *Daviesia* species (Brundrett & Abbott 1991). We found evidence of cluster roots in all species in the *Daviesia* group we investigated. The lack of cluster roots in *D. incrassata* subsp. *incrassata* was possibly a phenotypic response to an exceptionally wet and clayey habitat, and cluster roots were present in *D. incrassata* subsp. *reversifolia.* It would be of interest to also study the monotypic *Erichsenia* genus that belongs to the *Daviesia* group (Fig. 1d).

The group that is taxonomically closest to the *Daviesia* group, but not within Mirbelieae, is Bossiaeeae (Crisp & Cook 2003a). There are no records of any species producing cluster roots in this group, although several *Bossiaea* species have been studied in great detail (Abrahão *et al.* 2018). We also investigated *Bossiaea rhombifolia* at Davies Park NSW, and did not find cluster roots. Outside Mirbelieae, there are no reports of any Australian Fabaceae producing cluster roots. This might be a reflection of a lack of any investigation, as was the case for many species in the *Daviesia* group. However, Zemunik *et al.* (2015) studied nutrient-acquisition strategies in a range of species in this group, and would have noticed the formation of cluster roots. In a study by Hayes *et al.* (2014), none of the species in Mirbelieae outside the *Daviesia* group showed high leaf manganese concentrations, a proxy for carboxylate release in the rhizosphere (Lambers *et al.* 2015); this suggests that they do not produce cluster roots.

Compared with mycorrhizal roots, cluster roots are a superior P-acquisition strategy on severely P-impoverished soils (Lambers *et al.* 2018). It is likely that

Table 2. Summary of genera and some species in the *Daviesia* group; locations shown in Figure 2.

Genus	Species	Location (letters refer to Fig. 2)	Evidence for cluster roots	Comments
Daviesia	*angulata*	A; Lesueur National Park, WA	Yes	This study
	brevifolia	B; Cox's Scrub Conservation Park, SA	Yes	This study
	brevifolia	C; Broken Bucket Tank Bushland Reserve, Vic	Yes	This study
	chapmanii	D; Lesueur National Park, WA	Yes	This study
	cordata	n/a	Yes	Brundrett & Abbott (1991)
	corymbosa	E; on the Switzerland track in Wentworth Falls, NSW, in a *Banksia ericifolia* – *Allocasuarina* – *Hakea* – *Leptospermum* – *Kunzea* heath community	Yes	This study
	decurrens	n/a	Yes	Brundrett & Abbott (1991)
	divaricata	F; Lesueur National Park, WA	Yes	This study
	incrassata subsp. *incrassata*	G; Along Horner Road, Kundip Nature Reserve, WA	No	This study; habitat with wet clayey soil
	incrassata subsp. *reversifolia*	H; Along Hopetoun-Ravensthorpe Road, Kundip Nature Reserve, WA	Yes	This study
	physodes	n/a	Yes	Lambers *et al.* (2019)
	teretifolia	I; Fitzgerald River National Park near Hopetoun, WA	Yes	This study
	ulicifolia	J; Minnehaha Reserve near Katoomba, NSW	Yes	This study
Gompholobium	*aristatum*	K; Alison Baird Reserve, WA	Yes	This study
	floribunda	L; Davies Park in Springwood, NSW, in a *Banksia serrata* and *Corymbia gummifera*-dominated woodland community	Yes	This study
	tomentosum	M; Alison Baird Reserve, WA	Yes	This study
Sphaerolobium	*daviesioides*	N; Hamersley Drive, Hopetoun, on the way to the Fitzgerald River National Park, WA	Yes	This study
Viminaria	*juncea*	n/a	Yes	Lamont (1972); Walker *et al.* (1983)

the evolution of this trait in the *Daviesia* group allowed *Daviesia* to rapidly radiate in severely P-impoverished environments (Crisp *et al.* 2017). Cook *et al.* (2014) explored three explanations for biodiversity hotspots: small geographic range, geographic overlap and time for species accumulation. We surmise that the high diversity of *Daviesia* in south-western Australia compared with the rest of Australia also reflects the abundance of severely P-impoverished soils in the region, where cluster roots are of pivotal importance. Cluster roots are pervasive in Proteaceae (Purnell 1960; Shane & Lambers 2005), which also have their greatest diversity in south-western Australia (Pate *et al.* 2001). It is puzzling, however, why *Daviesia* diversified abundantly, whereas two sister genera in the *Daviesia* group (*Viminaria* and *Erichsenia*), of which at least *Viminaria* produces cluster roots, are monotypic.

CONCLUSION

This survey has expanded our knowledge of species and genera that produce cluster roots, and revealed that it is more common in Fabaceae than previously known. *Daviesia* is the most diverse fabaceous genus in Australia (with *ca.* 130 known species), followed by *Pultenaea* and *Gastrolobium*, with ca. 110 species in both genera (Crisp *et al.* 2017). Further work is needed to explore if cluster roots are also found in the other two large Australian Fabaceae genera (*Pultenaea* and *Gastrolobium*).

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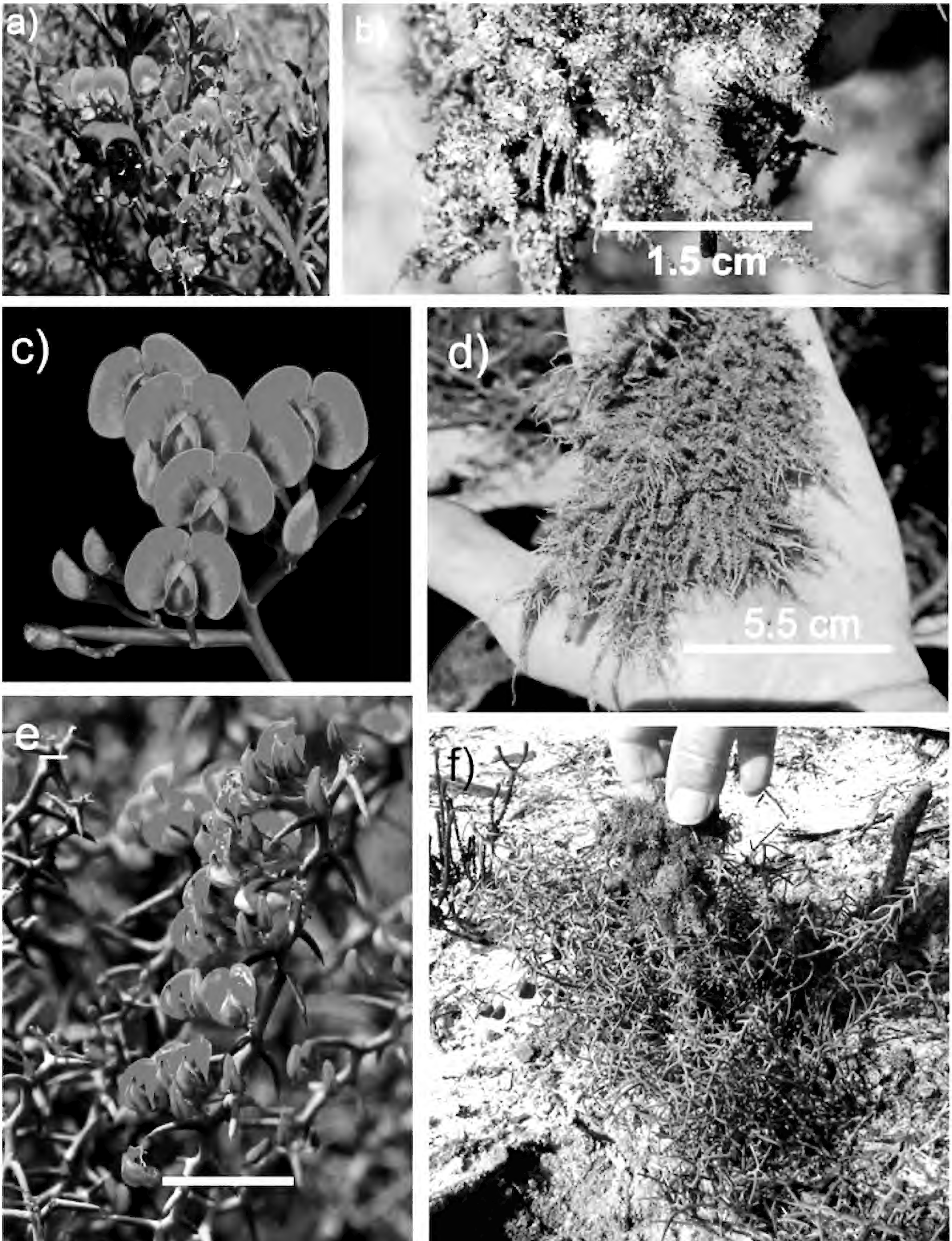

Figure 3. Representative diversity of *Daviesia* with cluster roots: a, b) *Daviesia physodes,* c, d) *Daviesia divaricata,* e, f) *Daviesia incrassata* subsp. *reversifolia.* Photos by authors, except d) by Kevin Thiele. Scale bars are 1 cm unless otherwise stated.

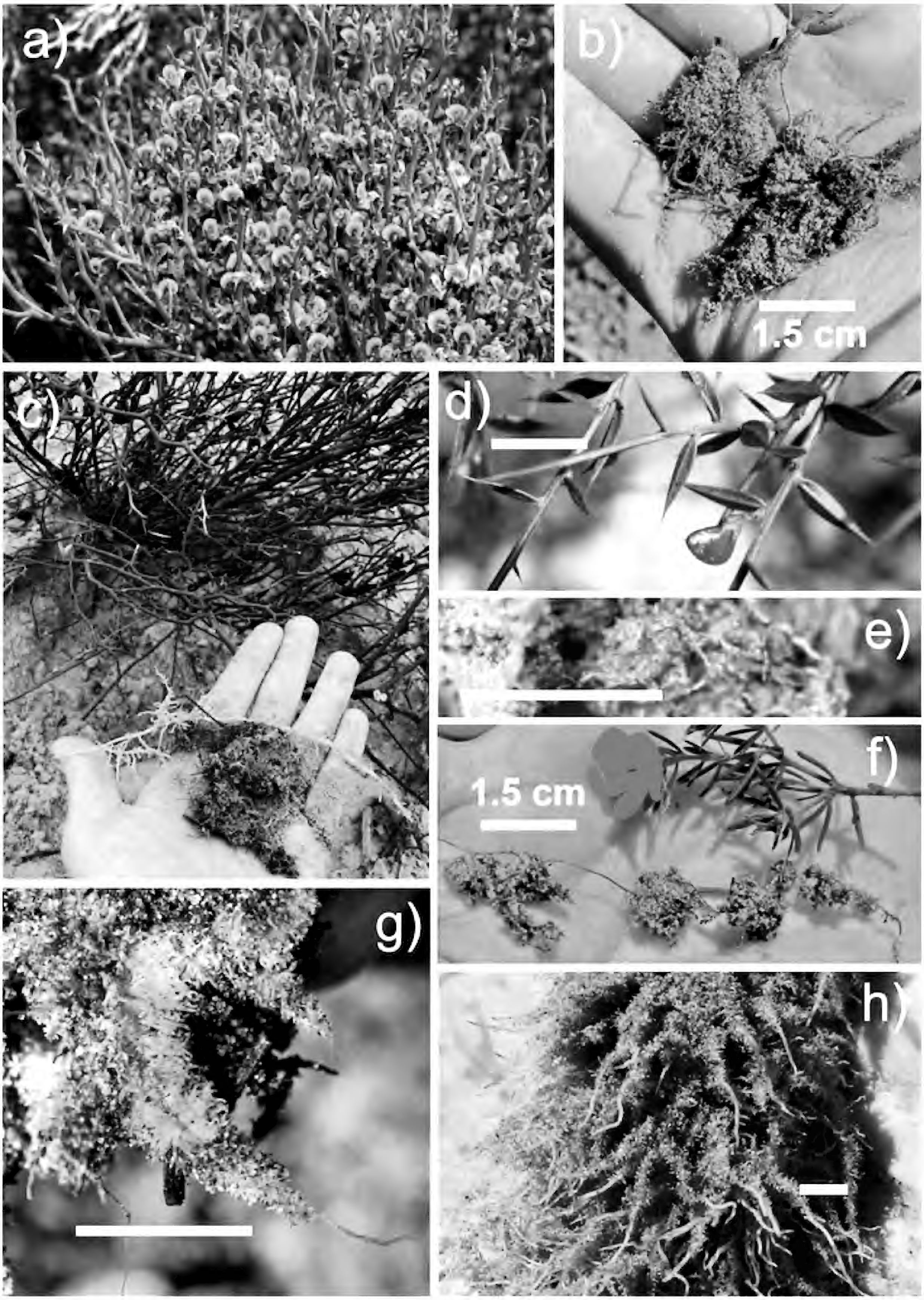

Figure 4. Representative diversity of *Daviesia* and allies with cluster roots: a–c) *Daviesia brevifolia*, d, e) *Daviesia ulicifolia,* f) *Gompholobium tomentosum*, and close up images of cluster roots from g) *Daviesia physodes,* h) *Daviesia divaricata.* Scale bars are 1 cm, unless otherwise stated.

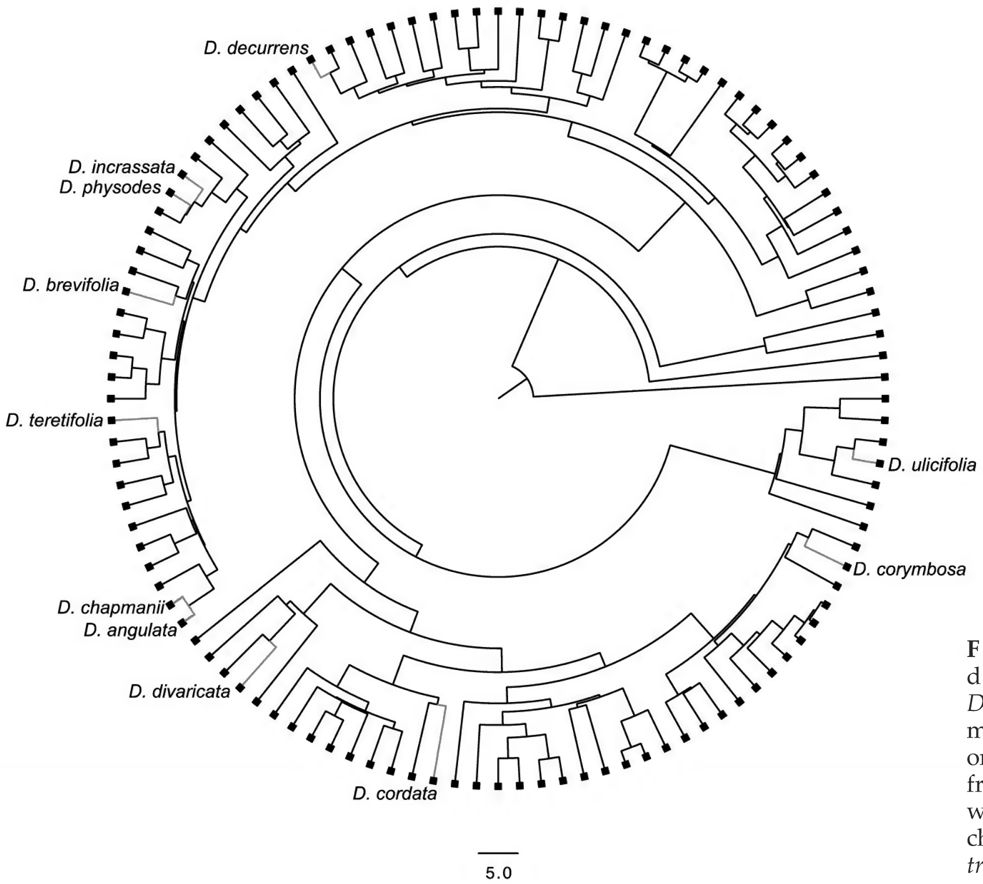

Figure 5. Currently documented species of *Daviesia* exhibiting cluster root morphology highlighted in red on the species-level phylogeny from Crisp *et al.* (2017), which was based on ITS and two chloroplast markers (*ndhF* and *trnL*).

(permit no. 10008523), and South Australian Department of Environment, Water and Natural Resources (permit no. G25787-4) for their permission to examine plants on land under their administration. Material in New South Wales was collected on local council land in accordance with local legislation.

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Discussion on 'A. R. Wallace in the light of historical method' by John van Wyhe

CHARLES H. SMITH [1]*, GEORGE BECCALONI [2], JAMES D. WILLIAMS [3] & DEREK PARTRIDGE [4]

[1] *Western Kentucky University, Bowling Green, KY 42101, USA*

[2] *The Charles Darwin Trust, 31 Baalbec Road, London, N5 1QN UK*

[3] *School of Education and Social Work, University of Sussex, Falmer, Brighton BN1 9RH, UK*

[4] *University of Exeter, Harrison Building, North Park Rd, Exeter EX4 4PY, UK*

* *Corresponding author: ✉ charles.smith@wku.edu*

Summary

The recent article by historian John van Wyhe purports to identify seventeen 'myths' concerning the life and work of naturalist Alfred Russel Wallace. Here we briefly describe what we feel is wrong with them, and refer to published literature that extend these arguments. Our objections do not extend to the 'historical method' van Wyhe adopts, but instead to the way he has ignored the criticisms of peers to the extent of not even acknowledging their scholarly articles.

Keywords: Alfred Russel Wallace, historical method, history of science, biography

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INTRODUCTION

In John van Wyhe's (2020) article devoted to Alfred Russel Wallace (1823–1913), 'in light of the historical method,' we question his conclusions although not the 'historical method'. We are perplexed that van Wyhe has ignored the many scholarly studies, which have carefully examined his published arguments and commonly found them seriously flawed.

Van Wyhe treats what he believes to be seventeen misunderstandings concerning Wallace that he says he has refuted in his previous articles and books. We here examine each in turn, if briefly, with reference to subsequent studies that have assessed van Wyhe's arguments.

DISCUSSION OF THE 'MISUNDERSTANDINGS'

1 & 2: *'Wallace was [not] working-class or from the opposite side of the social spectrum than Charles Darwin.' and 'As a youth Wallace was [not] forced to leave school early at age 14 because the family money ran out.'*

Van Wyhe's almost total devotion to Wallace's work in the Amazon and Malay Archipelago before he returned to England in 1862 leads him to ignore or misunderstand that most 'working-class hero' referrals by Wallace researchers relate to Wallace later becoming a hero *to* the working-class due to his extraordinary attention to their various unfair treatments. Whereas it is true that Wallace could probably claim a higher social standing than the then average man, all evidence points to his family's inclusion among the economically 'common.' When Wallace was five, they abandoned their country cottage near Usk, Wales—the one van Wyhe refers to as the 'grandest in the area'—to move to a series of modest rentals in Hertford. Things did not get better, either, as he 'finally left school at Christmas, 1836' (likely, sometime before 18 March 1837, per Raby 2001; Wallace 1905, i, p. 79) to join his brother John in London. Wallace is not clear as to the exact reason for the latter move, but earlier in his account, after describing the family's financial trials and tribulations while in Hertford, he states: 'It will thus be seen that we were all of us very much thrown on our own resources to make our way in life' (Wallace 1905, i, p. 15). He may or may not have been 'removed' from school before completing his term, but it is clear enough that the family underwent financial strain. On the school-leaving age matter, Williams (2020) notes that, contrary to van Wyhe's words, 'the raising of the school-leaving age to 14 did not happen until 1918,' and 'Wallace's employment as a teacher [at Leicester] would have been completely unrelated to the age [he] left school' [at Hertford]. Furthermore, the Hertford institution was aimed toward folks of modest means, and Wallace's employment there was to help pay the relatively low fee for his schooling.

3 & 4: *'Wallace went to the Amazon as a specimen collector [not to investigate the causes of biological evolution].'*

That Wallace intended to support his field studies as a collector is not an issue, but contrary to Van Wyhe's statement, there is sufficient evidence that he was also interested in investigating the 'transmutation question',—which van Wyhe dismisses without a mention. He does cite the well-known 1847 letter to Bates, but misrepresents it. Wallace (1847) wrote: 'I begin to feel rather dissatisfied with a mere local collection—little is to be learnt by it. I should like to take some one family,

to study thoroughly—principally with a view to the theory of the origin of species'. There is no implication here he is speaking solely of insects, or of Great Britain alone, as attention to entire families would require study of overseas species (the British fauna is depauperate, even with respect to mainland Europe). What more clear statement of intent is possible? Then there is Wallace's 'Sarawak Law' paper, containing the famous words: 'The great increase of our knowledge within the last twenty years, both of the present and past history of the organic world, has accumulated a body of facts which should afford a sufficient foundation for a comprehensive law embracing and explaining them all, and giving a direction to new researches. It is about ten years since the idea of such a law suggested itself to the writer of this paper, and he has since taken every opportunity of testing it by all the newly ascertained facts with which he has become acquainted, or has been able to observe himself' (Wallace 1855, p. 185). For discussion of the many additional lines of evidence originating during 1848–1858 that bear on this matter and clearly demonstrate that van Wyhe's statement is spurious, see Costa (2013a, b; 2014a, b; 2019a, b), Costa & Beccaloni (2014), Beccaloni (2014a, b).

5: *'There is no evidence that Wallace was searching for any mechanism or solution.'*

There is abundant evidence, which is given in full in the references cited above. Wallace's exact understanding of the concept of 'adaptation' is beside the point: no one has ever implied that Wallace's search for an evolutionary model was based on his then-perception of what an 'adaptation' might be in an evolutionary sense (McKinney 1972; Smith 2012, 2015a). Indeed, here van Wyhe has fallen into a misappreciation: Wallace would come to recognize, as Darwin had, that the *mechanism* of evolutionary change involved a *process of adaptation,* and not just an end-result of having adaptations (i.e. that came about directly in response to some other possible causal influence such as climate). It appears that van Wyhe is suggesting that because Wallace went into the field with an incorrect interpretation of the dynamic concept of adaptation, he could not have been seeking an understanding of how species changed over time. This level of restriction of focus is not useful. Buffon, Maupertuis, Erasmus Darwin, Lamarck, and others, though slaves to various understandings and terminologies of their times, were all trying to identify how a sustained process of organic change might take place.

6: *'Wallace [did not] write his essay on the island of Ternate…'*

This perhaps cannot be proved absolutely one way or another at present, though Beccaloni (2019) and Beccaloni *et al.* (2019) provide substantial evidence that the event took place in the village of Dodinga on the island of Gilolo. Of more import, however, is van Wyhe's resolve that Wallace's memory is not to be trusted on these matters. Van Wyhe conceals that the memory of events has two main components: the ability to recall the qualities of an event itself, and an ability to attach such remembrances to absolute labels involving dates, and the proper names of the people and places connected to them (Bradburn *et al.* 1987; Thompson *et al.* 1997)—both are well known among students of self-biography. In the first sense Wallace's memory—of the qualitative content of events, places, and things—was in his own time remarked upon as being excellent (some of the reviews of his autobiography actually criticize him for including *too much* detail, and a reading of the work reveals many impressively detailed descriptive passages; Smith 2020). Conversely, his ability to recall exact dates and names was not so good, and many related errors appear in his writings (Smith 2016; 2019a, b). Nevertheless, it is one thing to complain that he mistook a year or ship's name, and quite another to dismiss his recollection—on six different published occasions (Smith 2015b)—that he specifically sent the Ternate essay out on the next mail from that town only a few days after writing it (i.e. on 9 March 1858, not 5 April). As to his not mentioning Malthus in the Ternate essay, and therefore possibly having been unaware of him at that time, many other people he might have mentioned in that work, including Lyell, are not singled out either. Van Wyhe is technically correct in pointing out the lack of contemporary period proof of this, but as it stands we have a choice of three explanations: (1) that a person with a demonstrably excellent memory had a lapse concerning such an important matter; (2) that Wallace lied about this; and (3) that all is merely as it appears to be. Historical work is about weighing *all* the kinds of available evidence, not just ones that suit a particular agenda.

7: *'Wallace's original theory was in some ways similar and parallel to Darwin's, but also quite different…'*

This matter of alleged similarity is a much more complicated issue than it initially appears to be. There have been attempts to claim that what the two of them said in the joint Linnean Society presentation (Darwin & Wallace 1858) contained fundamental differences, but these attempts have largely been disposed of through closer analysis (e.g. Kottler 1985). As a result, the original appraisals (such as Darwin's famous words 'Even his terms now stand as heads of my chapters') of similarity still seem largely apt. Even so, some other differences between Darwin's and Wallace's contributions in their 'joint' paper have indeed been noted, for example by Kutschera (2003), including their contrasting positions on Lamarckian effects, and Darwin's identification of sexual selection. It may be that what Wallace *didn't* say in his essay ultimately matters most in this context. Wallace does not mention humankind in the work, but nevertheless almost everyone has assumed, possibly incorrectly (see Smith 2004, 2008, 2019a) that his natural selection model was meant to apply to the development of our 'higher' attributes, just as it did to animal qualities. This should give pause, because if he was still confused on this issue and avoiding the question, his choices of direction in the years following require serious re-evaluation.

8 & 9: '*Wallace recollected decades later that he wrote the essay 'in order to send it to Darwin'.'*

Both of these items contain so many dubious conclusions and conjectures—and dependence on 'poor recollection'—that only a brief reply can be given here. There is no contemporary evidence that Wallace's packet was a reply to Darwin's letter dated 22 December

1857. That he *did* send it to Darwin is beyond question, but apparently this was largely—or *entirely*—because he knew Darwin was a friend of Charles Lyell, whose opinion he really was seeking. Concerning 'beliefs that trace back to', the only proposal that Wallace's packet was a response to Darwin's letter was made by Raby (2001) concerning a *My Life* passage: 'I [Wallace] asked him if he thought it sufficiently important to show it to Sir Charles Lyell, who had thought so highly of my former paper' (Wallace 1905, i, p. 363). Raby interpreted this as period historical evidence of Wallace knowing this only because Lyell's opinion had been conveyed in Darwin's letter; however, a more likely interpretation is that with these words Wallace of 1905 is reminding his readers of Lyell's part in the whole story, which had only been mentioned once several pages earlier and not alluded to again. Wallace's strange phraseology is characteristic of his uneven writing style (as discussed by Charles Peirce in a 1906 book review: Peirce 1906; Smith 2014a), but beyond this the words 'thought so highly of [my essay]' appear in a letter Wallace sent to his mother in October of 1858 describing the recent events (Smith 2016); Wallace likely had the letter handy fifty years later when he was writing his autobiography. Most probably, Wallace's packet was already in the March 1858 mailbag by the time he opened Darwin's letter (a day or few days later). The discussion concerning the mail steamer dates is a distraction, as we ultimately do not care what ships went where and when, but how the mail itself moved through the system. There is no way to know this—although we do know that a letter Wallace sent in March 1858 (to Henry Walter Bates's brother Frederick) reached England in early June. The packet to Darwin must have been hand-sorted several times on its way from Ternate to Down, and who can say what kinds of delays there may have been? The whole steamer-schedule business tells us little in the end, appealing only to conspiracy theorists and Darwin apologists.

10: *'Wallace's essay was published in accordance with the standards of the day.'*

We fail to see what conclusion is drawn here. Blaming Beddall (1968) for making the 'lack of consent' observation is beside the point: the work *was* published without his consent (including, as he complained later in print—rather deliberately, at least five times—without his having been offered an opportunity to examine proofs). He later recollected that he had said nothing about publishing his essay when he sent it out (remarks confirmed by Darwin's words in a letter written at the time), and whether it was published 'in accordance with the standards of the day' contributes little to the matter.

11: *'Wallace's and Darwin's contributions were communicated by Charles Lyell and Joseph Dalton Hooker to the Linnean Society on 1 July 1858 'in the order of their dates'…'*

The evidence for this seems sketchy, and although it may well be true that the practices of the time weighed in Darwin's favour, this is somewhat like saying slavery was acceptable in the early nineteenth century. Thus, we may understand, as dispassionate witnesses, how the decisions were made, but, considering that Wallace was the initiating figure (and that he was not consulted about the decision to publish), we may still believe that something unseemly took place. In three recent papers Partridge (2015, 2017, 2018) draws attention to the dynamics of publication for the 1858 essays. In these works he focuses on the apparently single-minded efforts by Darwin's friends to establish his priority *in print*, and that Darwin's contribution to the presentation consisted largely of outdated thoughts from his initial words in 1844 (leaving further questions as to the meaning of 'priority' in this instance).

12: *'It was seldom described as the Darwin–Wallace theory of evolution…'*

Wallace's contributions to *natural selection theory* were as wide-ranging as Darwin's, if not nearly so minutely laid out. It remains to be seen whether his ideas on evolution *in general* will eclipse Darwin's; perhaps we will find out once they are more fully explored (Smith 2012), a process that is taking longer than it should.

13: *'Wallace was [not] the greatest field biologist of the 19th century.'*

Field biology as a discipline and occupation is a twentieth century phenomenon, contrasting with typical nineteenth century efforts by enlisting a more experimental approach (as opposed to mere observation and collection). Thus we can best identify Wallace as a 'field *naturalist*,' the word 'field' being inserted to distinguish the approach of his early years from armchair observers, museum specialists, and other kinds of nature-focused workers such as astronomers (as found in the early issues of *Nature*). Van Wyhe's complaint that it is hyperbole to rate Wallace as the 'greatest field naturalist' of the nineteenth century (or perhaps, ever) requires an assessment of who else was in the running for such recognition. If such a vote had been made during the nineteenth century, the geographer Humboldt likely would have this honour, with a few votes possibly going to geologist Darwin. More recently, Wallace has risen in such stakes not only because his was a more personal effort and lasted longer, but because the 'prizes' he secured, including the theory of natural selection, were equally numerous and have ultimately proved more substantial (Beccaloni 2020). Moreover, he was one of the few naturalists who published important scholarly papers while still in the field. Van Wyhe implies that the 'greatest' label is nothing more than hagiography, but how are we to judge this?

14: *'He is [not] also the father of biogeography.'*

Van Wyhe is either being lawyerly here, or does not appreciate the interrelation of the fields of biogeography and zoogeography, or the history of their development. Most responsible sources now refer to Wallace as either the 'father' of zoogeography, or of *historical* (also known as evolutionary) biogeography alone. Until recently, most practitioners of zoogeography have been in one sense or another systematic zoologists who turned to a historio-spatial perspective to help complete their evolutionary models of particular species groups. By contrast, since the beginning of the nineteenth century, the typical 'biogeographer' has been botanically, geographically, or ecologically trained, and been concerned largely with ecological settings. These boundaries have increasingly blurred, as well they should. If there are any 'fathers' of

biogeography they are probably early nineteenth century workers such as Humboldt and the Candolles; but they had no model of evolution that provided a critical long-term time dimension. Wallace and Darwin did, and it was the former who led the way in the spatial realm. Wallace may therefore reasonably be recognized, at the least, as a father of historical biogeography alone, or alternately of zoogeography.

15: *'His book **The Malay Archipelago** has [not] never been out of print.'*

In a 30 December 2015 email to van Wyhe in response to the 2015 note, CHS included:

> There appear to be no new English-language *printings* of MA by Macmillan (or other publishers) after the 1922 one [and before the 1962 one], but this does not mean that it was 'out of print' at that point; *British Books in Print* still lists it as being in print as of its 1936 volume [also, in its 1924, 1928, and 1932 ones; the listing disappears after 1936]. When someone refers to something as still being 'in print' as of a particular date, it doesn't mean that there has been a new imprint created then, just that the last [-dated] imprint, however old, is still available for ordering through the publisher.

Meanwhile, according to the bibliographic database *FirstSearch*, imprints of the title were issued in Japanese in 1931, 1942 and 1954, and in Chinese in 1933, 1935, 1939, and 1959; each of these undoubtedly remained 'in print' for at least several years afterwards, extending all the way to the 1962 Dover edition. There may well have been other editions not recorded in a library collection. The distinction between 'in print' and 'out of print' is clear enough that for several years there was a series called *Books Out of Print* that allowed the larger publishers, at least, a chance to formally declare at some point (probably in most cases when stock ran out, or requests for the title had dropped off) that a particular title was no longer available. So, being 'in print' has to do with availability, and essentially nothing to do with the most recent imprint date. Some titles are still available for thirty years or more after their last (or only) imprint date, something CHS can personally attest to from years of experience as a science materials purchaser.

16: *'At the end of his life he was [not] the most famous scientist in the world.'*

The argument has been that he was either *among* the most-famous/'greatest,' or *the* most-famous/greatest of those *still living* at the time of his death. Van Wyhe's remarks notwithstanding, there is sufficient defense for such a surmise. Smith (2014b) and Beccaloni (2013) both present data bearing on this question. Smith's examination of his name in *HathiTrust* records over the final period of his life, found that among then-living scientific figures only Lord Kelvin had significantly more mentions. However, Lord Kelvin died in 1907, leaving Wallace the highest 'scorer' for the following six years. Re-running the survey for 1900–1909 and 1910–1919, yields essentially the same results (the closest challengers were Robert Koch, Wilhelm Ostwald, Wilhelm Wundt, and John Muir). Fiske, mentioned by van Wyhe, often wrote on evolution, but was more of a philosopher and historian, and died in 1901; Lankester, Burbank, Galton and Crookes, are also mentioned but come up short, though Lodge has a similar tally. Using Google's Ngram Viewer, it can be shown that by Wallace's later years he was being cited more often than Hooker, Huxley and Owen (the last two of whom had died in the 1890s), and had drawn about even with Lyell (also deceased). An analysis of mentions of Darwin, Huxley, Lankester, and Wallace in *The Times* over 1880–1920 confirms these results (Fig. 1). Looking at the number of mentions of prominent scientists in the several hundred newspapers covered by the British Library newspaper database over 1905–1915 shows that—beyond Lord Kelvin and Lodge—Madame Curie, Lord Lister, Koch, John Muir, and Wallace were similarly frequently mentioned. Plenty of incidental evidence backs up these numbers (including that Wallace was, during the period following Lord Kelvin's death in 1907, more than three times more frequently referred to as *the*—as opposed to 'a', 'that', 'this', 'our', etc.—'Grand Old Man of Science' in the British Library online newspaper database than was any other figure). Admittedly none of this proves outright that Wallace was, absolutely, the greatest scientist of his time, at the least he should not be so summarily dismissed as one of the very top candidates. Furthermore, van Wyhe's implication that the quotes given by Smith (2014b) refer only to obituaries is incorrect.

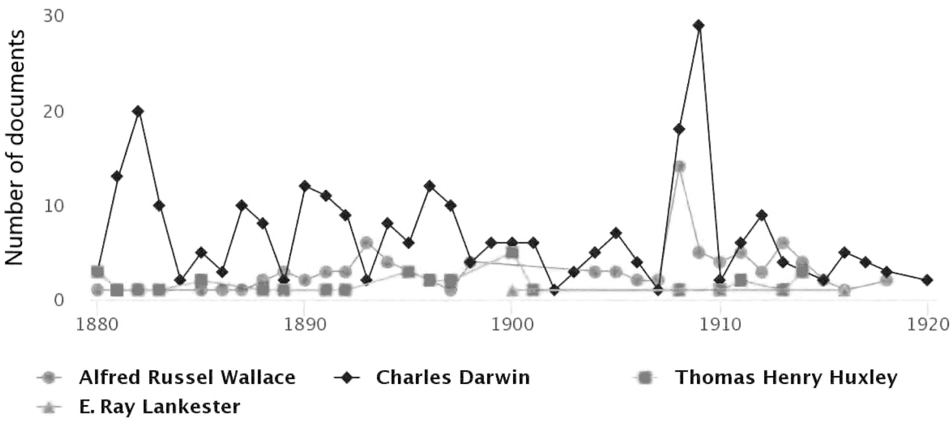

Figure 1. Number of articles per year in *The Times* mentioning four naturalists over 1880–1920.

17: *'He has [not] become strangely forgotten.'*

We tend to agree with van Wyhe that this is not really the case; even if Wallace *has* been forgotten to a degree not uncommon among historical figures, a fundamental question is to *what degree does he deserve <u>not</u> to be forgotten*. His was once a household name, and there were good reasons for this.

SUMMARY

Our replies to van Wyhe's remarks are intended, not to prop up Wallace, but to return productively to the question of what happened during his life, and how this may be important to us. Perhaps the most troubling part of the way van Wyhe applies the 'historical method' is that it ends up being too backward-gazing. The real importance of history is its ability to cast light on the present, and the possibilities of the future, if only we could come to consensus on all the facts of the past. Unfortunately, we are a long way from achieving this, and indeed even if we eventually can, the mission of historical revelation will not have been completed: much of what took place in the past is unrecognized now not only because it was unrecorded or has been forgotten, but because it is no more understood now than it was at the time. This is especially true of intellectual history. For figures as intellectually creative as Wallace undoubtedly was, we submit that one should have especially good reasons to object to the manner of his representation, especially if at odds with the records of the time. While we applaud van Wyhe's support of this particular method of doing history, it appears to us that his choice of Wallace as whipping boy in this context was ill-chosen. We are certainly not unamenable to revisionist interpretations of Wallace's life and work, but these should incorporate more than assertions.

Wallace was by anyone's standards a remarkably inventive thinker, and differed from most other scientists in history in having secured a substantial social reputation, especially in his later years. This, together with the romance of his travels and his broad and often provocative interests, explains the current rise of a popular attraction to him. We don't believe this interest is a bad thing—as long as it is based on the truth—so the changing 'Wallace narrative' over time is neither surprising, nor to be regretted. Is there any reason to think that the opinions of Wallace in his own time were any more valid, or useful, than are any such opinions offered today? Individual historians do not get to make such decisions: their job is to record, as accurately as possible, both the facts and the opinions. This doesn't mean that we need to encourage unsupported hero worship, but historians should not push conclusions based on preconceptions and incompletely reported research. Van Wyhe frequently states that he is the first historian to subject Wallace to critical inquiry, but many past historians have taken on Wallace as a primary subject: for example, Gerald Henderson, H. Lewis McKinney, Malcom Jay Kottler, Michele Malinchak, Jane Camerini, Jean Gayon, Michael Shermer, and Martin Fichman.

Whereas van Wyhe is free to come to his own conclusions on the matters he deals with, it is not acceptable to denigrate contrary pieces of evidence, nor is it proper to ignore the criticisms of peers by not acknowledging their scholarly articles.

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